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EGGS AND LARVAE OF THE PACIFIC HAKE *MERLUCCIUS PRODUCTUS*

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EGGS AND LARVAE OF THE PACIFIC HAKE, *MERLUCCIUS PRODUCTUS*

By ELBERT H. AHLSTROM and ROBERT C. COUNTS, *Fishery Research Biologists*

The larva most abundant in the extensive monthly plankton collections of the California Cooperative Oceanic Fisheries Investigations is that of the hake, *Merluccius productus* (Ayres) 1855. The collections are made primarily to study the distribution and abundance of sardine eggs and the rate of survival of sardine larvae; information on other species of present or potential commercial importance is a byproduct. This paper is the second in a series describing the eggs and larvae of the more important species.[1]

The California Cooperative Oceanic Fisheries Investigations are sponsored by the California Marine Research Committee, and are being carried on by the Scripps Institution of Oceanography of the University of California, the California Department of Fish and Game, the California Academy of Sciences, the Hopkins Marine Station of Stanford University, and the South Pacific Fishery Investigations of the United States Fish and Wildlife Service.

Hake larvae are taken over almost all of the area being surveyed, from northern California to Cape San Lucas in Baja California, and offshore for more than 350 miles. Although neither the north-south nor the offshore extent of spawning of this species has been delimited, it is unlikely that spawning outside the survey area is of much importance. Since hake have a rather short spawning season, most larvae are taken during the 3-month period February through April.

In his revision of the species of *Merluccius*, Norman (1937) recognized seven species: *M. merluccius* (Linnaeus) from the coasts of Europe, northwest Africa, and the Mediterranean; *M. bilinearis* (Mitchill) from the Atlantic coast of the United States; *M. hubbsi* (Marini) from the east coast of South America; *M. gayi* (Guichenot) from the coasts of Chile and Peru; *M. capensis* Castelnau from off South Africa; *M. australis* (Hutton) from off New Zealand; and *M. productus* (Ayres) from the Pacific coast of North America. *M. angustimanus* Garman, described from off Panama, was placed by Norman as a possible synonym of *M. gayi;* it may be a valid species, however. Unfortunately, we did not have access to the revision of American hakes (whitings) by Isaac Ginsburg (Fishery Bulletin 96) until too late to incorporate his findings in this paper. See page 329.

Merluccius productus can be distinguished from other species of the genus by the following combination of morphological characters:

1. A more slender body form than that of any other species, with the possible exception of *M. hubbsi;* depth is 7 to 7⅔ in standard length as compared with 5 to 6¼ for all other species except *M. hubbsi* (5¾ to 8(?)).

2. A high gill-raker count (4 or 5 + 14 to 17); only *M. gayi* has a comparably high count.

3. Several more rays in the second dorsal and anal fins than any species except *M. australis* (D.[2] 39 to 42; A. 40 to 43).

A literal translation of the name *Mercluccius productus* would be "drawn-out sea pike" or "slender sea pike."

Of the above species, *Merluccius merluccius*, *M. gayi*, *M. bilinearis*, and *M. capensis* are of considerable commercial importance. These species are sold in the fresh-fish trade, or are used for meal and oil. Various references mention the fact that the flesh of these species is well-flavored when fresh, but spoils rapidly. Apparently this is characteristic of the genus. Pacific-coast fishermen have found the flesh of *M. productus* to be similar; however, no regular commercial fishery has been established for this species. At one time it was used for animal food by mink farmers, but was deficient in some nutrients. Recently, the hake has been utilized to some extent as a fish-hatchery food. It seldom appears in the Pacific-coast fresh-fish markets.

Reports on the great availability of hake by commercial fishermen, and the large annual spawn, as determined by the California Cooperative

[1] Descriptions of the methods and materials used for collecting and standardizing the net tows, clearing and staining specimens, and measuring body proportions of larvae are given in Fishery Bulletin 97 (Ahlstrom and Ball, 1954).

Oceanic Fisheries Investigations, give evidence that there is a large untapped fishery resource in the hake. The demand for protein foodstuffs may, in the near future, force the exploitation of this hitherto unused and potentially large resource. This would entail some research into the capture, proper handling, preparation, and marketing of the species. Perhaps much of this information could be gathered from a study of the processing and marketing procedures developed for the several species of hake that now support commercial fisheries.[2]

Employees of the Scripps Institution of Oceanography and the California Department of Fish and Game cooperated in the collection of data at sea. The whole staff of the South Pacific Fishery Investigations of the Fish and Wildlife Service contributed to this study. The authors thank especially John C. Marr, Rolf Bolin, and James Böhlke for critically reading the manuscript, James R. Thrailkill for preparing the graphs and distribution charts.

EGGS AND LARVAE OF OTHER SPECIES OF *MERLUCCIUS*

The egg and larval stages have been described for several species of *Merluccius*. A number of descriptions have been published of the eggs and larvae of *M. merluccius*, among which the following four accounts are particularly noteworthy:

1. Raffaele (1888) published descriptions of the egg and yolk-sac larvae, obtained by artificially fertilizing eggs stripped from hake caught in the Bay of Naples.

2. J. Schmidt (1907) described and figured the development of hake larvae from 4.25 mm. to 31 mm. in length (13 specimens) from material obtained off Ireland, Bay of Biscay, Scotland, and the Skaggerak.

3. Ehrenbaum (1905–9) supplemented Schmidt's descriptions with material from the Jutland Auszen-ground.

4. D'Ancona (1933), in Fauna e Flora del Golfo di Napoli, gives a résumé of previous work and a group of 8 figures of larvae 4 to 32 mm. in length, obtained from the Mediterranean.

The eggs and larvae of *Merluccius bilinearis*, the hake occurring off the east coast of the United States, were described by Kuntz and Radcliffe (1917), but some of the descriptions and figures in their paper are inaccurate. For example, a late-stage egg (fig. 53) is shown with more than 70 myomeres, and a yolk-sac larva (fig. 54) has only 45 myomeres. Furthermore, figures 64 and 65, included in the series of *Poronotus triacanthus*, are based on specimens of *Merluccius bilinearis* (Pearson, 1941, called attention to this discrepancy, but suggested that these figures might be young of *Urophycis*.). These latter figures were copied without change by Bigelow and Welsh (1925) in Fishes of the Gulf of Maine, but are omitted from the revision of this work by Bigelow and Schroeder (1953).

The early development of *Merluccius capensis* (egg and yolk-sac larval stages) was described by Matthews and Jager (1951). A figure of a later larval stage is given in a short paper by Hart and Marshall (1951).

Neither the eggs nor the larvae of *Merluccius productus* have been described previously.

EGGS OF *MERLUCCIUS PRODUCTUS*

Embryonic development of hake eggs has been studied in both living and preserved material. The following descriptions are based on preserved material, since such samples are examined much more frequently than living specimens. Two important differences between living and preserved material should be noted: (1) Living hake eggs have a glassy transparency and the yolk material is almost colorless, while preserved eggs appear opaque and the yolk material is more highly colored; and (2) living embryos contain evanescent pigments, especially yellow pigments, that are destroyed in preservation (Melanophores are not so affected, however).

General description.—The hake egg is pelagic. It is spherical, has a tough, transparent, unsculptured shell membrane, and contains a single, rather large oil globule. The yolk material is clear, homogenous, and of a dark straw color; however, it may appear granular after being enclosed by the germ ring. The egg often appears cloudy or opaque in the stages preceding blastopore closure. This probably is due to mechanical rupture of the delicate vitelline membrane surrounding the yolk, which allows the yolk material to escape into the perivitelline space. The following size measurements are based on 200 eggs taken at ran-

[2] A San Francisco plant operator recently has been granted a permit for experimental reduction of hake to meal and oil.

dom from preserved samples: The average diameter of the hake egg is 1.12 mm. (range, 1.07 to 1.18 mm.); the average diameter of the oil globule is 0.30 mm. (range 0.27 to 0.34 mm.); the diameter of the yolk is approximately 1.00 mm.; and the width of the perivitelline space is approximately 0.06 mm. A comparison of the size of the egg and of the contained oil globule in *Merluccius productus*, *M. bilinearis* (data from Kuntz and Radcliffe, 1917), *M. merluccius* (data from Raffaele, 1888) and *M. capensis* (data from Matthews and Jager, 1951) follows:

Species	Diameter (in millimeters) of—	
	Egg	Oil globule
M. productus	1.07–1.18	0.27–0.34
M. bilinearis	0.88– .95	.19– .25
M. merluccius	.94–1.03	.27
M. capensis	1.03	.16

The time required for embryonic development of hake eggs has not been determined. It may be similar to that of the sardine. This conclusion is based on finding two or three stages of egg development in many samples. From studies on the sardine (*cf.* Ahlstrom 1943), such stages have been shown to represent as many days' spawning. Kuntz and Radcliffe (1917) attributed an incubation period of only 48 hours to the silver hake (*M. bilinearis*), Raffaele (1888) reported an incubation period of 60 to 70 hours for *M. merluccius*, while Matthews and Jager (1951) gave 60 hours as the time required for the embryonic development of *M. capensis*. None of these investigators supplied temperature data.

In discussing the development of the hake eggs, we shall divide the embryonic period into three stages:

Early—from fertilization to closure of the blastopore (fig. 1, *a* and *b*).

Middle—from closure of the blastopore to the time that the separating tail begins to curve laterally away from the embryonic axis (fig. 1, *c* and *d*).

Late—from the time that the tail is curved away from the embryonic axis to the time of hatching (fig. 1, *e* and *f*).

Early-stage eggs.—In early-stage hake eggs (fig. 1, *a* and *b*), the yolk is clear and unsegmented, and the oil globule is situated at the vegetative pole. The developing egg floats with the oil globule uppermost, as do most pelagic eggs. At the time of blastopore closure, the oil globule is situated immediately adjacent to the blastopore, close to the tail of the embryo. It keeps this position throughout the remainder of the embryonic period and during the yolk-sac larval stage. In this early stage, the embryo develops at a fairly rapid rate. When the embryonic shield has enveloped approximately three-fourths of the yolk, the embryo has a discernible eye. Just before blastopore closure, 10 to 13 myomeres are visible behind the head of the developing embryo. No pigment is found in this early stage.

Middle-stage eggs.—The best character for identifying middle-stage hake eggs (fig. 1, *c* and *d*) is the pigmentation that develops immediately after blastopore closure. Pigment appears in three areas, (1) on the oil globule, (2) on the head and dorsum of the embryo, and (3) on the yolk mass. The pigment on the oil globule is restricted to the hemisphere nearest the embryo. Pigment on the embryo is found first on the dorsum behind the head, where it outlines the myomeres adjacent to the head. It soon spreads over the head and most of the dorsum, although it is not equally dense in all parts, and the distal portion remains immaculate. The anterior portion of the yolk mass has a few scattered pigment spots, usually on either side of the head. At the termination of this stage, the tail has become partially separated from the yolk, and has started curving laterally away from the embryonic axis. The embryo has received its full complement of 50+ myomeres.

Late-stage eggs.—During this stage (fig. 1, *e* and *f*) the melanophores become restricted into several conspicuous patches of pigment, leaving portions of the embryo, previously with melanophores, immaculate. When viewed from above, the pigment on the embryo occurs in four areas: (1) on the head and four or five adjacent myomeres, (2) on the body just anterior to the anus, (3) on the body just behind the anus, and (4) about midway between the anus and the end of the notochord. We call the latter area the medio-postanal pigment area. The only conspicuous ventral pigment on the embryo is a counterpart to the dorsal patch in the medio-postanal region. Before hatching, some melanophores can be discerned in the peritoneum. The buds of the pectoral fins may be seen in late-stage eggs. The best single feature for identifying late-stage hake eggs is undoubtedly the characteristic pigmentation.

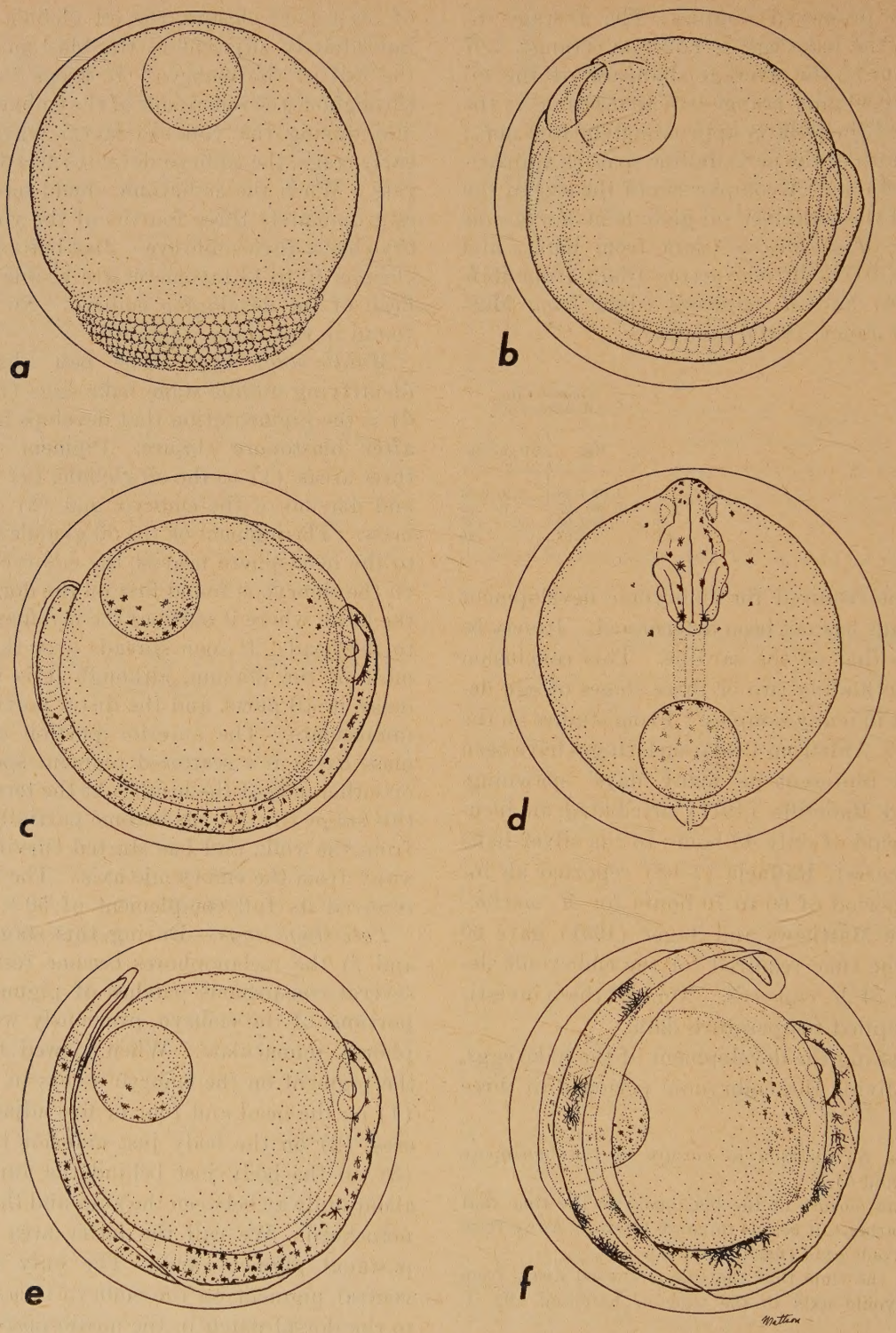

FIGURE 1.—Development of the egg of the hake, *Merluccius productus: a.* Early stage, at time of development of blastodermal cap; *b.* early stage, immediately preceding blastopore closure; *c.* middle stage, lateral view; *d.* middle stage, polar view; *e.* late stage, tail just beginning to twist out of plane of embryonic axis; *f.* late stage, just before hatching.

Other features that aid in identifying hake eggs at this stage of development are—

1. Number of myomeres—more than 50 can be counted.
2. Length of intestine—extends for about four-tenths of the total length.
3. Position of oil globule—situated near the anus.

In the waters inhabited by the Pacific hake, there are two other common species with rather similar eggs: the jack mackerel (*Trachurus symmetricus*), and the Pacific mackerel (*Pneumatophorus diego*). To avoid confusion in identification, table 1 has been prepared.

TABLE 1.—*Characters which aid in distinguishing the eggs and newly hatched larvae of hake, jack mackerel, and Pacific mackerel*

	Hake	Jack mackerel	Pacific mackerel [1]
EGG			
Size	1.07 to 1.18 mm.	0.96 to 1.02 mm.	1.05 to 1.08 mm.
Oil globule	Single—0.30 mm.	Single—0.25 mm.	Single—0.26 mm.
Yolk	Clear.	Segmented.	Clear.
Perivitelline space	Moderate (0.06 mm. wide).	Moderate (0.09 mm. wide).	Narrower than either hake or jack mackerel.
Pigmentation:			
Yolk	On yolk near head.	None.	Scattered on yolk.
Embryo	Dorsal pigmentation continuous in middle-stage eggs, separated into patches in late-stage eggs.	Dorsal pigment extends most of length of embryo; ventral pigment occurs behind anus; pigment seldom occurs forward of the eyes.	Double dorsal row of pigment spots extends forward between the eyes; no ventral pigment.
Number of myomeres	51–54.	24.	31.
YOLK-SAC LARVAE			
Pigmentation	Collects in patches.	Dorsal and ventral retained.	Dorsal pigment migrates ventrally.
Oil globule	In rear of yolk sac.	Under head in forward portion of yolk sac.	In rear of yolk sac.

[1] Data taken, in part, from Fry 1936.

LARVAE OF *MERLUCCIUS PRODUCTUS*

State of development at hatching.—The hake hatches in a relatively undeveloped condition. It begins its postembryonic existence before the mouth forms and before the eyes become pigmented. The young of most other fish with pelagic eggs, including the sardine, anchovy, Pacific mackerel, jack mackerel, and tunas, are in a similarly undeveloped state at hatching.

A group of approximately 200 hake larvae, representative of the size range obtained in the plankton hauls, was selected for detailed study. The larvae were chosen at random from samples that adequately covered their geographical and seasonal distribution. The specimens were cleared and stained by a procedure modified from that described in Hollister (1934).[3] Meristic counts can be determined accurately from specimens prepared in this manner, and the sequence of ossification of vertebrae and other bony parts can be followed. However, stained specimens are not satisfactory for observing the sequence of pigment changes, and for this purpose other larvae, taken at random, were used.

The period of larval development is considered to extend from hatching to the completion of fin formation, but the end of the larval stage is not sharply defined in the hake. The size at hatching, determined from preserved material, is approximately 2.4 mm. All fins except the pectorals have their full complement of rays by the time the fish is 20 mm. long. The pectorals seldom have more than 2 or 3 rays differentiated at this size, with 7 formed by 25 mm., and probably the full complement when the larvae are about 30 to 35 mm. in length.

We shall trace the changes that occur during larval development in the following characters: (1) Changes in pigmentation, (2) changes in body form, (3) sequence of ossification, and (4) sequence of fin formation.

CHANGES IN PIGMENTATION

There is considerable variation in the amount of pigment found on hake larvae of comparable size, especially noticeable in larvae under 10 mm. in length. In discussing pigment augmentation, we shall describe the usual pattern, not the aberrant. Larvae with the most intense, as well as those with the sparsest, pigmentation were collected more often in the southern part of the survey area than elsewhere.

The newly hatched larva (fig. 2*a*) has a pigment pattern similar to that of a late-stage egg. Before yolk-sac absorption is completed, however, the pigment has migrated or coalesced to

[3] Improvements on Hollister's technique were suggested by Evans (1948) and Clothier (1950).

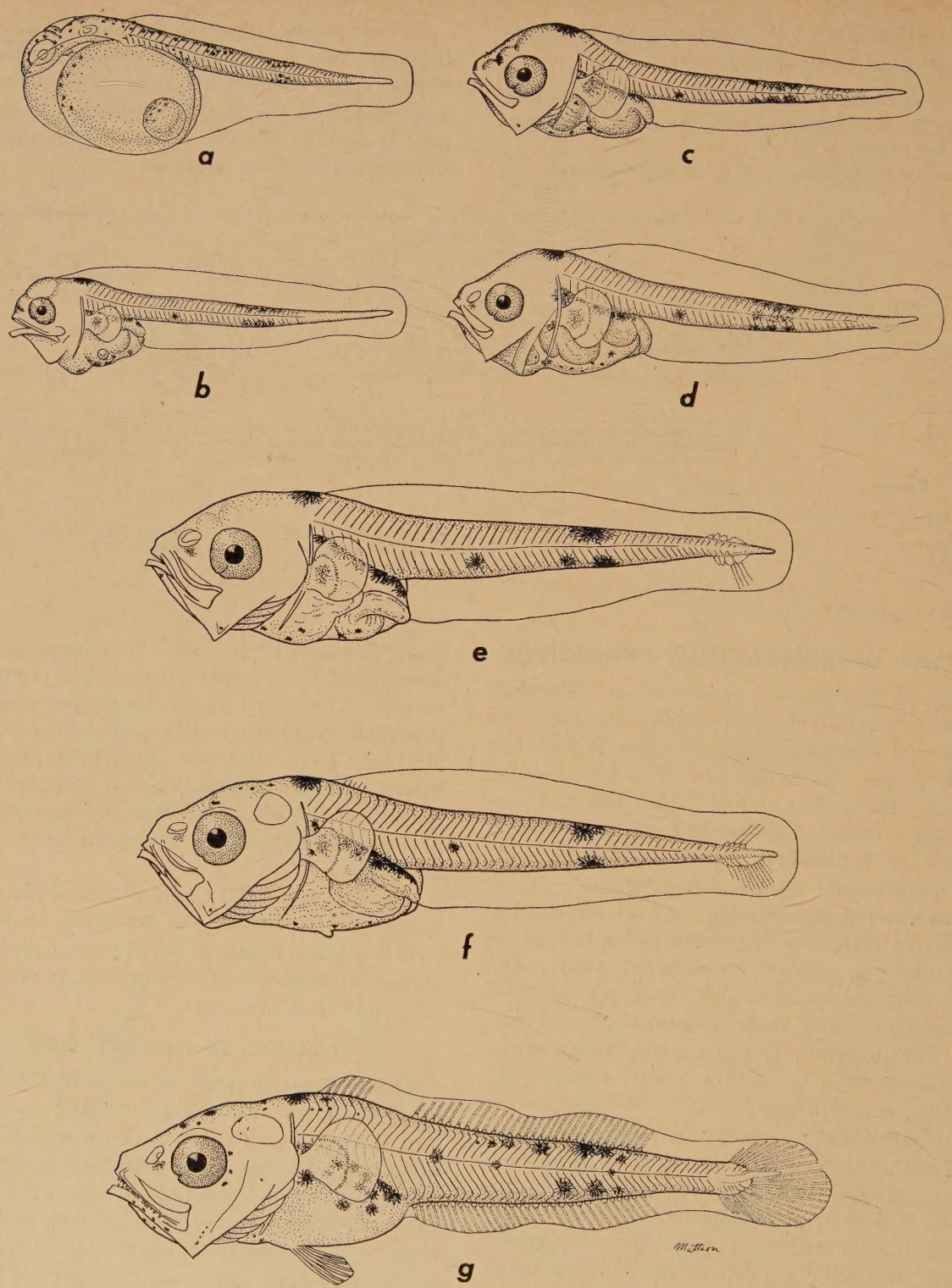

FIGURE 2.—Development of the larva of the hake, *Merluccius productus: a.* Yolk-sac larva, 2.4 mm. long, immediately after hatching; *b.* larva 3.0 mm. long; *c.* larva 4.3 mm. long; *d.* larva 4.7 mm. long; *e.* larva 6.3 mm. long; *f.* larva 7.7 mm. long; *g.* larva 10.1 mm. long.

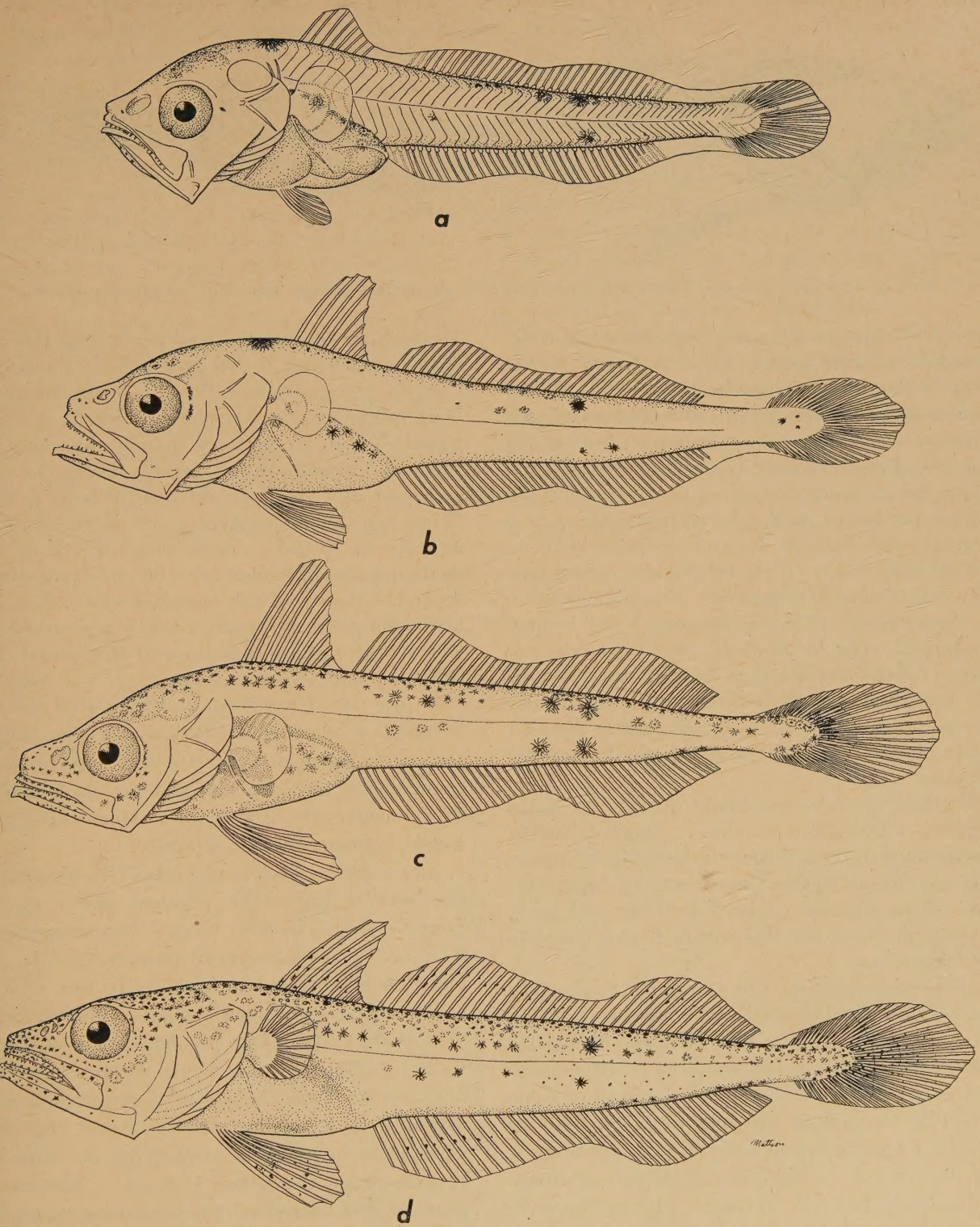

FIGURE 3.—Development of the larva of the hake, *Merluccius productus: a.* Larva 11.0 mm. long; *b.* larva 15.75 mm. long; *c.* larva 20.0 mm. long; *d.* early juvenile, 36.0 mm. long.

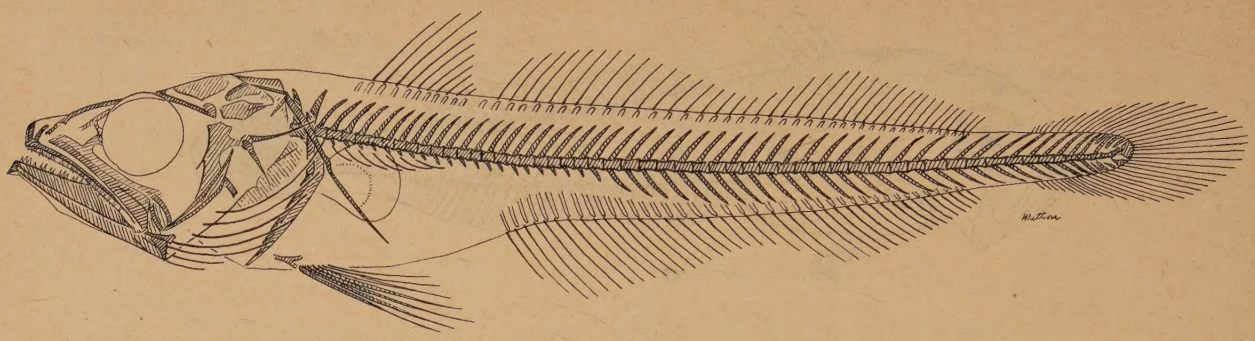

FIGURE 4.—Larva of hake, *Merluccius productus*, 25.0 mm. long, showing details of skeletal structure.

form the three conspicuous pigment areas characteristic of hake larvae: (1) a large spot on the back of the head, referred to hereafter as the occipital spot, (2) the conspicuous medio-postanal pigment area about midway between the anus and the end of the notochord (or base of caudal), and (3) a heavy concentration of pigment along the dorsal peritoneal wall. In addition, there is a frontal patch between the eyes, scattered spots on the ventral surface of the belly and a lateral spot immediately behind the anus. This pigmentation is characteristic of larvae between 3 and 10 mm. in length. The larva of *M. productus* does not have a caudal spot like that found on specimens of *M. bilinearis* and *M. merluccius*. Occasionally larvae are found with a row of lateral pigment spots between the anus and the medio-postanal pigment area.

Pigment is added gradually during the larval period. Until about 10 mm. in length, most of the increase in pigmentation is in the head region. Between 10 and 20 mm. there is a rapid augmentation of the pigment on both the body and head. Pigmentation of the fins occurs during the late larval period.

Head pigmentation.—In young larvae the only conspicuous pigmentation on the head is the large occipital spot. This is usually a single, stellate melanophore. But a few scattered small melanophores are found on the top of the head of some larvae at the end of the yolk-sac stage. By 10 mm. in length, a cap of discrete pigment spots is usually present on the crown. On larvae of approximately 13.5 mm. in length, pigment appears along the premaxillary and mandible, and a conspicuous vertical bar forms behind the eye. On larvae 20 mm. in length, pigment spots are generally distributed along the top and sides of the head except in the opercular area behind the eye. Meanwhile, the occipital spot has become less conspicuous, although it still may be distinguished.

Body pigmentation.—There is little change in body pigmentation between 3 and 10 mm. in length, but on larvae more than 10 mm. long the pigment increases rather rapidly along the dorsum, and later along the sides of the body as well. When the dorsal pigment starts augmenting, it appears to spread in both directions from the medio-postanal pigment area, but only posteriorly from the region of the occipital spot. The last areas along the dorsum to become pigmented are at the origin and termination of the second dorsal fin. A continuous band of dorsal pigment from the tip of the snout to the base of the tail is found on larvae as small as 16.5 mm. in length. Larvae larger than this show a marked increase in number of melanophores and ventral spreading of pigment to the lateral line. Meanwhile, peritoneal pigment spreads laterally.

As the larvae become more heavily pigmented, the several important pigment areas of the younger stages tend to become less conspicuous. The medio-postanal group concentrates into several lateral melanophores, usually one or two above and as many below the lateral line on either side of the body. This pigment group still may be conspicuous on some larvae 20 mm. long (fig. 3*c*), but on other larvae is distinguished with difficulty at a smaller size than this (fig. 3*b*). The group has lost its identity by the time the juvenile stage is reached (fig. 3*d*). The lateral pigment spot immediately behind the anus, seldom conspicious at any size, is indistinguishable from other scattered ventral pigment spots in older larvae (fig. 3*c*).

Ventral pigmentation is never as conspicuous in hake larvae as dorsal pigmentation. The mel-

anophores on the ventral surface of the abdomen remain few in number and gradually disappear. Only during the late larval period is there a noticeable increase in pigmentation below the lateral line, and even then it is sparse along the ventral margin of the body.

Fin pigmentation.—The fins never become heavily pigmented in larval hake. There are usually either scattered pigment spots or a single conspicious stellate spot on the fleshy base of the larval pectoral fins. In some larvae under 20 mm. in length, a few small pigment spots have been observed bordering the central rays of the caudal fin. By 36 mm. in length, the caudal fin is much more heavily pigmented, especially along the median rays. The first dorsal has pigment spots outlining its rays, especially anteriorly. The second dorsal has some inconspicuous lines of pigment along its rays, and there is even less pigment on the anal fin. The ventral fins usually lack pigment, but occasionally a heavily pigmented larva will have pigment on the ventral fin even at formation.

CHANGES IN BODY FORM

The hake larva is moderately elongate, with the greatest body depth at or near the pectoral fin, and with the body narrowing abruptly behind the anus. The digestive tract underlies only the forward part of the body, the distance from snout to anus being approximately 42 percent of the standard length. The intestine has a single loop, readily observable in small larvae before it is obscured by overlying musculature.

Measurements made on the group of larvae studied included the following: Standard length, head length, diameter of eye, greatest body depth, and distance from snout to anus. The data are summarized in columns 3 to 7 of table 2. The measurements and counts in this table are average values based on 10 or fewer specimens (number of specimens listed in column 2).

TABLE 2.—*Measurements and meristic counts of hake larvae*

Size	Number of specimens examined	Average measurements (in millimeters)					Meristic counts							
		Standard length	Head	Eye	Depth	Snout to anus	Vertebrae	Branchiostegal rays	Caudal fin	Ventral fins	First dorsal	Second dorsal	Anal fin	Pectoral fins [1]
(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)	(14)	(15)
3.0–3.4 mm	7	3.2	0.73	0.30	0.95	1.4								LP
3.5–3.9 mm	5	3.7	.86	.36	1.02	1.6								LP
4.0–4.4 mm	10	4.3	1.00	.40	1.07	1.8	1.0							LP
4.5–4.9 mm	10	4.6	1.09	.46	1.18	2.0	1.8	0.7						LP
5.0–5.4 mm	10	5.0	1.14	.49	1.38	2.2	2.1	2.2						LP
5.5–5.9 mm	10	5.7	1.36	.56	1.50	2.6	3.4	4.3	0.3					LP
6.0–6.4 mm	10	6.3	1.46	.60	1.51	2.6	3.9	4.4	.7					LP
6.5–6.9 mm	5	6.7	1.74	.68	1.66	3.0	4.8	5.4	2.4					LP
7.0–7.4 mm	10	7.1	1.89	.70	1.81	3.2	6.9	6.4	8.3	0.6				LP
7.5–7.9 mm	5	7.8	2.00	.74	1.80	3.4	8.0	6.0	6.8	2.2				LP
8.0–8.4 mm	10	8.2	2.19	.78	1.81	3.6	15.1	6.5	13.2	2.5	1.4			LP
8.5–8.9 mm	10	8.6	2.22	.85	2.09	3.8	29.6	6.6	15.7	3.6	2.7	3.6	6.0	LP
9.0–9.4 mm	10	9.1	2.53	.88	2.18	4.0	45.4	7.0	19.6	5.5	4.6	7.5	10.8	LP
9.5–9.9 mm	3	9.7	2.57	.90	2.23	4.0	49.3	7.0	18.3	5.3	6.0	21.7	27.7	LP
10.0–10.4 mm	10	10.1	2.75	.98	2.35	4.5	52.9	7.0	23.9	6.7	6.4	26.7	28.1	LP
10.5–10.9 mm	7	10.6	2.99	.97	2.49	4.9	53.0	7.0	25.1	6.9	6.7	30.1	30.7	LP
11.0–11.9 mm	6	11.3	3.03	1.07	2.47	5.0	53.5	7.0	28.5	7.0	7.3	32.5	34.0	LP
12.0–12.9 mm	5	12.5	3.36	1.14	2.62	5.4	53.8	7.0	30.0	7.0	7.8	33.2	36.0	LP
13.0–13.9 mm	6	13.4	3.82	1.27	2.85	5.9	52.8	7.0	34.0	7.0	8.5	37.0	37.3	LP
14.0–14.9 mm	4	14.5	3.95	1.30	2.92	6.3	53.0	7.0	33.5	7.0	9.0	37.2	38.0	LP
15.0–15.9 mm	5	15.5	4.40	1.36	3.12	6.6	53.0	7.0	36.8	7.0	10.0	38.8	40.0	LP
16.0–16.9 mm	2	16.7	4.80	1.45	3.10	7.0	53.5	7.0	39.0	7.0	11.0	40.0	41.5	0.5
17.0–17.9 mm	4	17.5	4.85	1.40	3.32	7.4	53.0	7.0	39.8	7.0	10.5	40.0	41.0	.5
18.0–18.9 mm	6	18.3	5.28	1.63	3.42	7.7	53.0	7.0	40.5	7.0	10.5	39.7	41.0	.2
19.0–19.9 mm	2	19.6	5.60	1.55	3.80	8.2	54.0	7.0	42.5	7.0	11.0	40.5	42.5	.0
20.0–20.9 mm	4	20.3	5.95	1.65	3.80	8.4	53.8	7.0	42.0	7.0	10.5	40.2	41.2	.8
21.0–21.9 mm	5	21.2	6.04	1.66	4.18	8.9	53.8	7.0	41.6	7.0	10.4	40.0	41.6	2.2
22.0–22.9 mm	1	22.0	6.40	1.80	4.10	9.3	54.0	7.0	42.0	7.0	11.0	41.0	42.0	.0
23.0–23.9 mm	2	23.6	6.70	1.95	4.30	10.0	53.0	7.0	43.0	7.0	10.5	40.0	40.5	.0
24.0–24.9 mm	1	24.8	7.00	1.90	4.20	10.1	53.0	7.0	43.0	7.0	11.0	40.0	41.0	7.0
25.0–25.9 mm	1	25.5	7.30	2.20	4.50	11.0	55.0	7.0	44.0	7.0	11.0	42.0	40.0	7.0
40.0–40.9 mm	1	40.5	10.40	3.00	6.50	16.1	53.0	7.0	45.0	7.0	11.0	42.0	43.0	14.0
46.0–46.9 mm	1	46.2	13.00	3.20	8.00	16.8	53.0	7.0	44.0	7.0	11.0	42.0	43.0	15.0

[1] LP = larval pectoral.

Head.—The head grows at a constant rate in relation to the standard length during the larval period, increasing 0.30 mm. in length for each millimeter increase in standard length. This is shown in a regression of head length on standard length for larvae between 3 and 25 mm. in length

(fig. 5). The statistics describing the line fitted to the scatter of points by the method of least squares are given in table 3. It will be noted that actual measurements of head length are plotted against standard length in this graph. A quite different type of plot is obtained if head length, expressed as a percentage of the standard length, is plotted against the standard length (fig. 6). The latter is the usual method of dealing with body proportions in taxonomic studies. The head length is approximately 23 percent of the standard length in newly hatched larvae, increasing to 27 percent at 10 mm., and to approximately 28.5 percent at 20 mm. (table 4). This is not evidence of an accelerating rate of growth of the head as compared to standard length, although it might be misinterpreted as such. Rather it arises from the fact that the head length at hatching constitutes a smaller part of the standard length (23 percent) than the relation that obtains thereafter, i. e., a uniform rate of increase of head length to standard length of 30 percent.

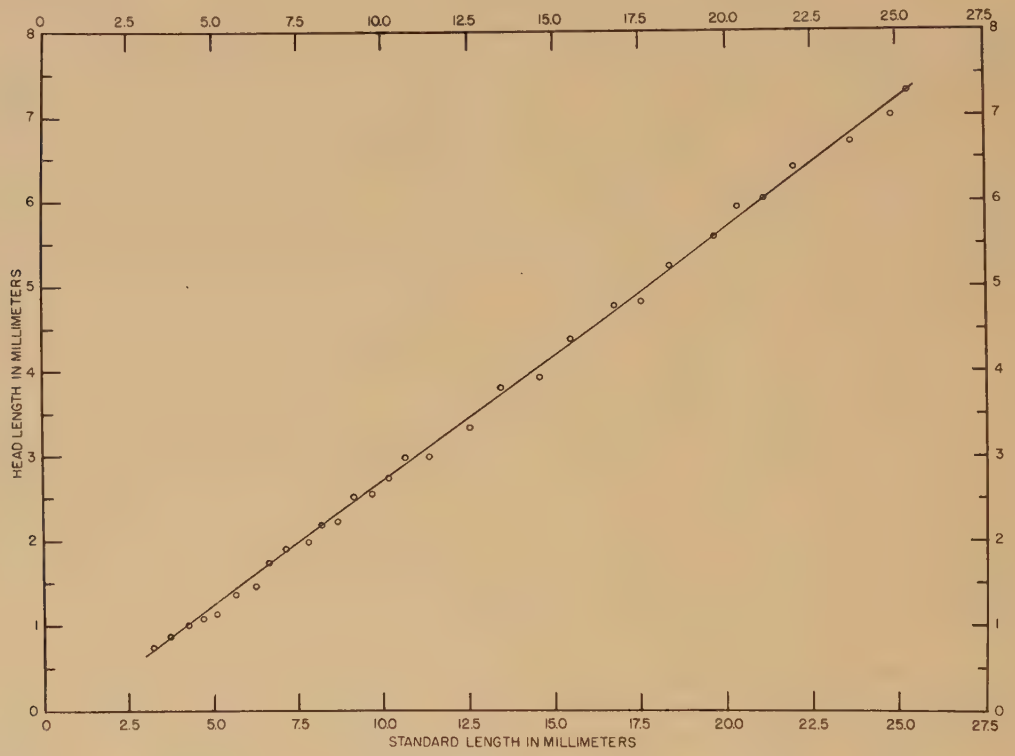

FIGURE 5.—Regression of head length on standard length. Each circle is the average of a group of measurements, often 10 (refer to table 2, columns 2, 3, and 4). Regression line fitted to the data by the method of least squares. Statistics describing the line given in table 3.

TABLE 3.—*Statistics describing regressions of body proportions on standard length for hake larvae*

Independent variable x	Dependent variable y	Size of larvae	$\bar{x}$	$\bar{y}$	N	b	a	$sy{\cdot}x$
		Mm.						
Standard length	Head length	3.2–25.5	12.50	3.45	31	0.299	−0.289	0.079
Do	Body depth	3.2–10.6	6.92	1.69	16	.207	.257	.063
Do	do	10.6–25.5	17.96	3.45	16	.142	.901	.119
Do	Eye diameter	3.2–12.5	7.47	0.71	18	.092	.030	.022
Do	do	12.5–25.5	18.96	1.59	14	.069	.285	.077
Do	Distance, snout to anus	3.2–25.5	12.50	5.37	31	.419	.129	.193

$\bar{x}$=mean of values of x.
$\bar{y}$=mean of values of y.
N=number of size groups.
b=rate of increase of y.
a=y intercept of regression line.
$sy{\cdot}x$=standard deviation from regression (standard error of estimate).

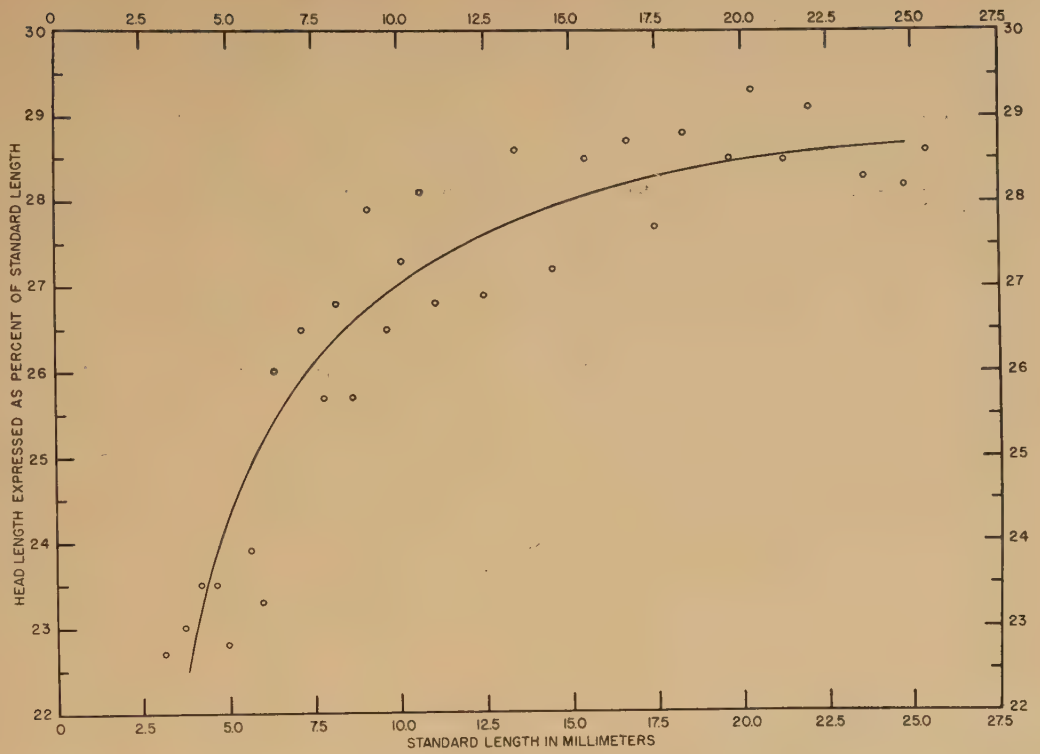

FIGURE 6.—Regression of head length, expressed as a percentage of standard length, on standard length. The curve is fitted from the statistics given in table 3.

TABLE 4.—*Body proportions of hake larvae*

Size	Standard length	Body proportions expressed as percentage of standard length			
		Head length	Eye diameter	Depth at pectorals	Distance from snout to anus
3.0–3.4 mm	3.2	22.7	9.3	29.6	42.7
3.5–3.9 mm	3.7	23.0	9.6	27.3	42.8
4.0–4.4 mm	4.3	23.5	9.4	25.1	42.7
4.5–4.9 mm	4.6	23.5	9.9	25.4	43.3
5.0–5.4 mm	5.0	22.8	9.7	27.4	43.3
5.5–5.9 mm	5.7	23.9	9.8	26.4	45.0
6.0–6.4 mm	6.3	23.3	9.6	24.1	42.3
6.5–6.9 mm	6.7	26.0	10.2	24.8	44.6
7.0–7.4 mm	7.1	26.5	9.8	25.4	45.2
7.5–7.9 mm	7.8	25.7	9.5	23.1	43.4
8.0–8.4 mm	8.2	26.8	9.5	22.1	43.4
8.5–8.9 mm	8.6	25.7	9.8	24.2	44.0
9.0–9.4 mm	9.1	27.9	9.7	24.0	43.8
9.5–9.9 mm	9.7	26.5	9.3	23.0	40.9
10.0–10.4 mm	10.1	27.3	9.7	23.3	44.9
10.5–10.9 mm	10.6	28.1	9.1	23.4	46.4
11.0–11.9 mm	11.3	26.8	9.5	21.9	44.5
12.0–12.9 mm	12.5	26.9	9.1	21.0	43.2
13.0–13.9 mm	13.4	28.6	9.5	21.3	44.0
14.0–14.9 mm	14.5	27.2	9.0	20.1	43.2
15.0–15.9 mm	15.5	28.5	8.9	20.2	42.7
16.0–16.9 mm	16.7	28.7	8.7	18.6	41.9
17.0–17.9 mm	17.5	27.7	8.0	19.0	42.4
18.0–18.9 mm	18.3	28.8	8.9	18.7	42.0
19.0–19.9 mm	19.6	28.5	7.9	19.3	41.5
20.0–20.9 mm	20.3	29.3	8.1	18.7	41.4
21.0–21.9 mm	21.2	28.5	7.8	19.7	41.9
22.0–22.9 mm	22.0	29.1	8.2	18.6	42.3
23.0–23.9 mm	23.6	28.3	8.2	18.2	42.5
24.0–24.9 mm	24.8	28.2	7.7	16.9	40.7
25.0–25.9 mm	25.5	28.6	8.6	17.6	43.1
40.0–40.9 mm	40.5	25.7	7.4	16.0	39.8
46.0–46.9 mm	46.2	28.1	6.9	17.3	36.4

Distance from snout to anus.—The anus is situated about four-tenths of the way back along the body, and it retains this relative position throughout the larval and juvenile stages. The distance from snout to anus increases 0.42 mm. for each 1 mm. increase in standard length (fig. 7 and table 3). Since the relation is constant, this is a useful taxonomic character. The distance from snout to anus in jack-mackerel larvae, for example, is nearly six-tenths of the standard length; hence jack-mackerel larvae could be separated from hake larvae on the basis of this character alone.[4]

Body depth (at pectoral).—The larva increases in depth more rapidly during the early part of its development than during the later part. The rate of increase in body depth for larvae between 3.2 and 10.6 mm. in length is 0.21 mm. for each 1 mm. increase in standard length, and for larvae between 10.6 and 25.5 mm. in length, the increase in body depth averages only 0.14 mm. for each millimeter increase in standard length

[4] Of course, there are other and more trenchant characters for separating these two species, such as the difference in number of vertebrae (24, as compared with more than 50), in pigmentation, in sequence of fin formation, and in numbers of fin rays.

(fig. 8 and table 3). As a result, the hake larva becomes progressively more slender with increase in size over 10.6 mm.

Eye.—The eye of the hake larva is round, with a ventral cleft developed in varying degree at the point of the choroid fissure. The eye does not grow at a uniform rate throughout the larval period. In larvae between 3.2 and 12.5 mm. in length, the diameter of the eye increases approximately 0.09 mm. for each millimeter increase in standard length, while in larvae between 12.5 and 25.5 mm. in length, the increase is only about 0.07 mm. for each millimeter increase in standard length. The distance from the snout to the anterior margin of the eye is about equal to the diameter of the eye.

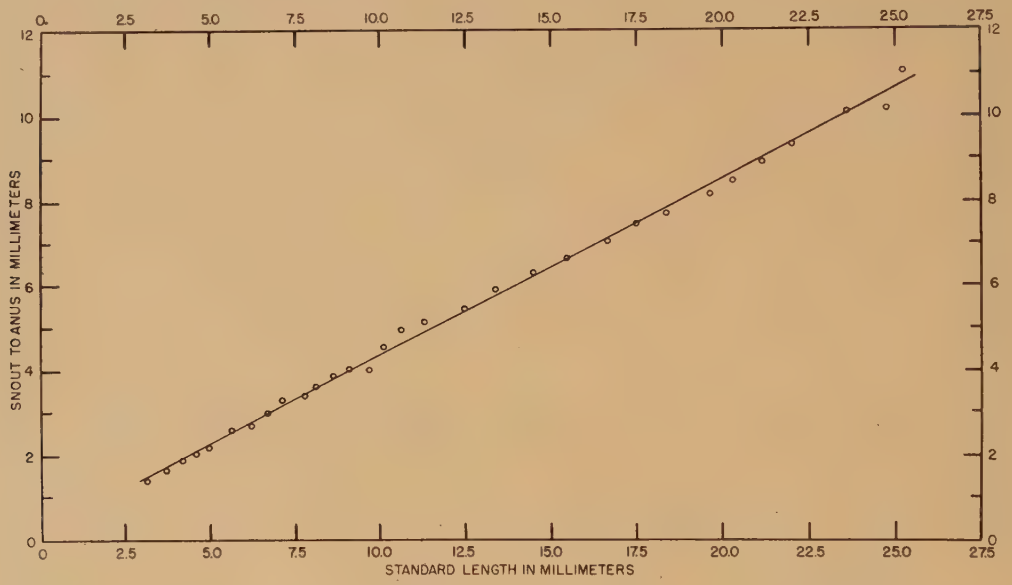

FIGURE 7.—Regression of the distance from snout to anus on standard length. Each circle is the average of a group of measurements, often 10 (refer to table 2, columns 2, 3, and 7). Statistics describing the regression line, fitted by the method of least squares, are given in table 3.

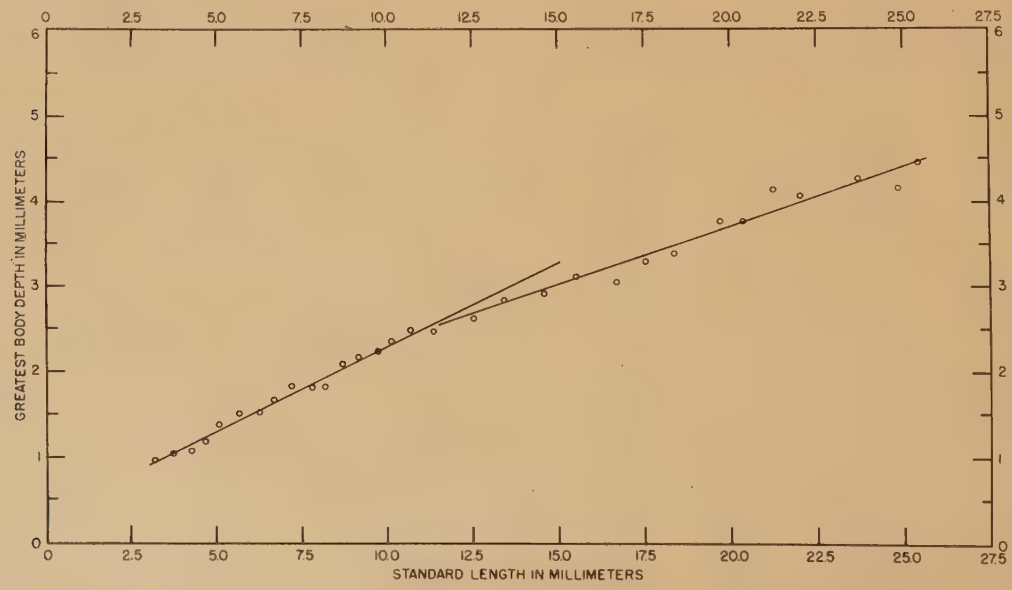

FIGURE 8.—Regression of greatest body depth on standard length. Each circle is the average of a group of measurements, often 10 (refer to table 2, columns 2, 3, and 6). Two regression lines have been fitted to the data by the method of least squares; one for larvae 3.2 to 10.6 mm. in length, the other for individuals 10.6 to 25.5 mm. in length. Statistics describing the two lines are given in table 3.

SEQUENCE OF OSSIFICATION

Vertebral development.—When any part of a vertebra (spine or centrum) takes alizarin stain, the vertebra is considered as forming, and is entered in our counts (table 2, column 8). In general, vertebral development is from anterior to posterior. However, there are some interesting deviations from this sequence which will be discussed below.

The first vertebral elements to show ossification are neural spines, the anterior one or two being formed on some specimens as small as 4 mm. in length. Development of vertebrae proceeds slowly until the larva achieves a length of 7.5 mm., whereupon it is greatly accelerated (fig. 10, and table 2, column 8). The centra do not show ossification in smaller specimens but once initiated, ossification of centra proceeds rapidly. As a result, the centra outstrip the neural spines in development, as is shown in the following table, based on four typical specimens.

Size of larva	Number of neural spines showing ossification	Number of centra showing ossification
7.0 mm	5	0
7.5 mm	7	0
8.5 mm	7	20
9.0 mm	9	35

Some specimens 8.5 mm. in length have all of the vertebrae developed, and all specimens 10 mm. long have the full complement.

The range in number of vertebrae for hake larvae on which accurate counts could be made was from 51 to 55, distributed as follows:

	Number of specimens
51 vertebrae	2
52 vertebrae	14
53 vertebrae	40
54 vertebrae	25
55 vertebrae	3

Although the sequence of ossification is, in general, from anterior to posterior, there are several exceptions. The neural and haemal spines of the third to sixth vertebrae preceding the urostyle begin to ossify before other vertebrae in this part of the body. These are the most posterior of the vertebrae with normally developed neural and haemal spines. However, the centra of these vertebrae are late in forming, being preceded by the centra of the penultimate and antepenultimate vertebrae.

The distinction between caudal and abdominal vertebrae (i. e., vertebrae with or without haemal spines) is evident when larvae have attained a length of approximately 9.5 mm. The range in number of abdominal vertebrae is from 23 to 26, with the majority of specimens having either 24 or 25. Soon after this distinction can be made, all abdominal vertebrae except the first six show an outward and downward growth of the parapophyses to form a bony roof over the abdominal cavity. This is a distinctive characteristic of the genus.

Branchiostegal rays.—Specimens of 4.5 mm. in length may show ossification of the upper branchiostegal ray. The sequence of ossification is from upper to lower. The full complement of 7 rays is found on some specimens as small as 7 mm., and on all specimens 9 mm. or more in length (column 9 of table 2).

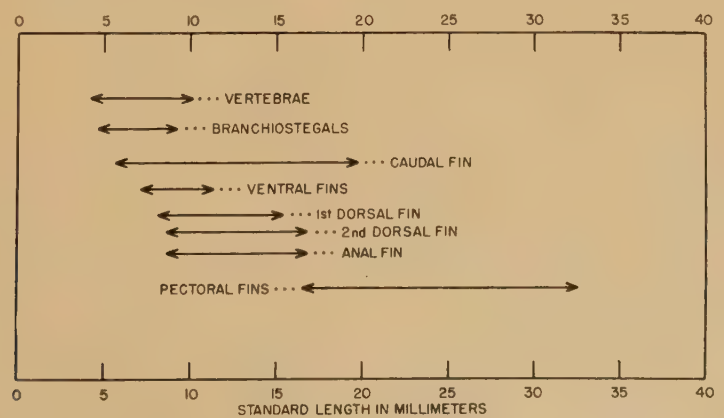

FIGURE 9.—Diagramatic summary of the sequence of ossification of basic meristic structures in hake larvae.

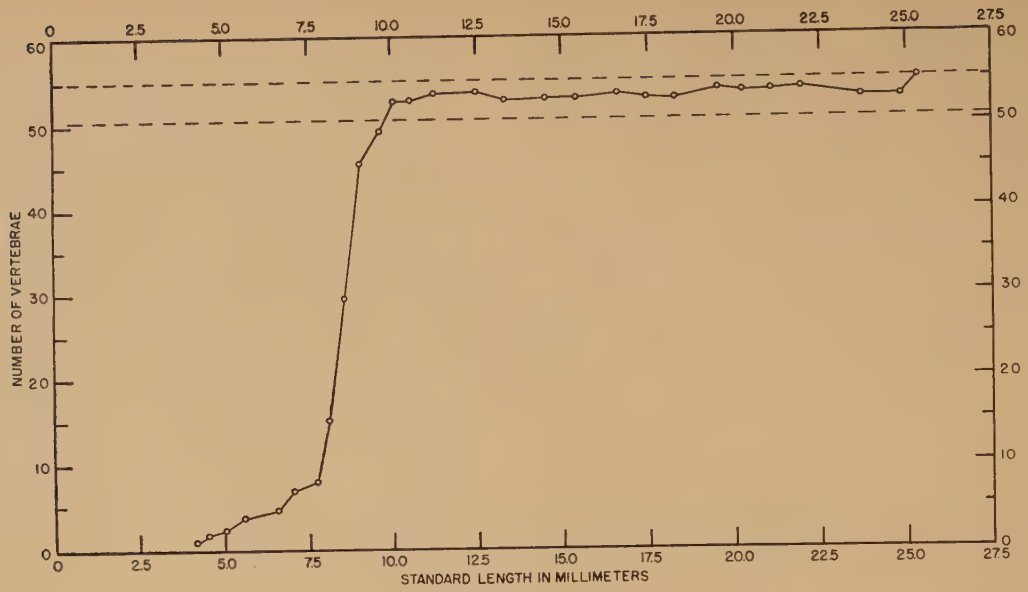

FIGURE 10.—Diagram of average number of vertebrae ossified in hake larvae between 3.2 and 25.5 mm. in length. Each circle is the average of 10 or fewer measurements (refer to table 2, columns 2, 3, and 8). When fully developed, the number of vertebrae ranges between 51 and 55.

Teeth.—Teeth are present on the premaxillary and mandible of larvae approximately 5 mm. in length. In small larvae, the mandible has a greater number of teeth than the premaxillary. By 11 mm. in length, the number of teeth on premaxillary and mandible is approximately equal, and on specimens larger than this, the premaxillary has the greater number. This may be seen from the following tabulation:

Size of larva	Count of teeth on one side	
	Premaxillary	Mandibl
6.8 mm.	4	5
7.0 mm.	4	7
11.0 mm.	9	9–10
17.5 mm.	22	15
20.5 mm.	45	40
40.0 mm.	78+	65+

The teeth are unevenly spaced, not uniform in size, and tend to occur in irregular groups. All of the teeth are either acutely conical or recurved. The anterior teeth are recurved and the posterior teeth are more nearly straight. The premaxillary and mandibular dentitions become biserial when the larva reaches approximately 30 mm. The teeth of the inner row on either jaw are longest and depressible posteriorly, as are those of the adults. A double row of vomerine teeth are found on larger larvae; we have not determined the exact size at which these form.

Gill rakers.—*Merluccius productus* has a higher gill-raker count than any other species of hake except *M. gayi*. Adult specimens of *M. productus* have 4 or 5+14 to 17 gill rakers. The first of the developing gill rakers are evident on larvae just under 10 mm. in length. For example, on a specimen 9.8 mm. in length, 6 gill rakers were present on the lower limb of the first arch; they were only short primordia, and none were developed on the upper limb. The counts on 8 specimens of graded size were as follows:

Size of larva	Gill-raker count	
	Upper limb	Lower limb
9.8 mm.	0	6.
12.0 mm.	0	8.
14.0 mm	0	11.
18.0 mm.	2	12.
23.5 mm	2	14.
25.0 mm	4	14.
41.0 mm.	4	15 or 16.
46.0 mm.	4	15.

The full complement of gill rakers is obtained by about 25 mm. in length.

Opercular and preopercular spines.—There are no spines evident on the head or preoperculum during the larval period. On the operculum are two needle-like ridges, which could be mistaken for spines (fig. 3).

Scales.—On hake larvae, the developing scales are highly deciduous, and the sequence of scale

formation has not been carefully studied. No scales were observed on larvae of 28 mm., but small scales were found on larvae 35 mm. in length. The 40.5-mm. and 46-mm. specimens were heavily scaled.

SEQUENCE OF FIN FORMATION

The sequence of fin formation in the hake is as follows:

1. Larval pectorals (without rays).
2. Caudal.
3. Ventrals (pelvics).
4. First dorsal.
5 and 6. Second dorsal and anal (simultaneously).
7. Pectorals (with rays).

These fins are discussed in order of their formation.

Larval pectoral fins.—The pectorals begin forming during the late embryonic period, and are fully developed on larvae about 3 mm. in length. They consist of a fleshy base and a wide undifferentiated membrane without rays. Rays do not appear until late in the larval period, and until then the pectorals are designated as larval fins.

Caudal fin.—The caudal fin of the hake has been classed as a "pseudocaudal" type by Barrington (1937) and other workers. The development of the caudal in the hake differs in a number of ways from typical homocercal caudal development as found in most fishes (for example, the jack mackerel, discussed in the first paper of this series). However, we cannot agree in all details with Barrington's interpretation of caudal development in the cod and related groups, as is pointed out in the following discussion.

The first evidences of caudal-fin formation are ventral and dorsal thickenings near the posterior tip of the notochord, found on some hake larvae as small as 4 mm. in length. Even in specimens only slightly larger than 4 mm. the rudiments of most hypural and epural elements can be distinguished. Rays do not appear (i. e., take stain) until the larvae are 5.8 mm. or more in length. The first rays form ventrally. Usually, when any rays can be distinguished, several have already ossified. Ray differentiation is initiated simultaneously on the penultimate and posterior hypurals. The 3 rays associated with the penultimate hypural differentiate anteriorly; the 6 rays on the posterior hypural differentiate posteriorly. Usually, when about 7 ventral rays are differentiated (3 on posterior hypural, 3 on penultimate hypural, and 1 anterior to the penultimate hypural), rays begin forming in the dorsal portion of the fin. The first dorsal ray to form will be the ray immediately adjacent to the urostyle. Differentiation of dorsal rays then proceeds anteriorly.

Soon after dorsal rays begin forming, the posterior portion of the notochord flexes upward and the posterior hypural assumes a terminal position. At first, the notochord extends almost 0.5 mm. beyond the posterior hypural plate, but it gradually shortens so that in specimens of 17.5 mm. in length it barely projects beyond the hypural.

The 9 rays associated with the posterior and penultimate hypurals have no dorsal counterparts; as interpreted by us, these rays represent the "homocercal" element in the development of a gadid caudal fin. This point was missed by Barrington. Ventral rays other than these 9 will be equal in number or 1 less than the total number of dorsal rays. This is true both during formation and after the caudal fin is fully formed. The following table based on selected specimens illustrates this:

Size of larva	Number of caudal rays originating--			
	Dorsally	Ventrally		Total
		Associated with 2 principal hypurals	Not associated with 2 principal hypurals	
6.3 mm.	0	4	0	4
7.8 mm.	3	8	3	14
9.0 mm.	6	9	6	21
11.0 mm.	9	9	9	27
13.0 mm.	13	9	13	35
14.4 mm.	15	9	14	38
18.0 mm.	16	9	15	40
21.4 mm.	17	9	17	43
170.0 mm. (approx.)	17	9	17	43

The average number of caudal rays found on larvae between 5.5 and 46 mm. in length is given in column 10 of table 2. The full complement of 42 to 45 caudal rays is present in specimens of approximately 20 mm. in length. Young hake as large as 46 mm. in length still have the posterior edge of the caudal rounded and not somewhat truncate as in adults.

The fully developed caudal fin is associated with the last 9 or 10 vertebrae (fig. 11). All except the last 3 of these appear to be normal vertebrae with long, sharply inclined neural and haemal spines. We have noted earlier that these spines ossify earlier than surrounding vertebral struc-

tures. The antepenultimate and the penultimate vertebrae have normal centra, but modified spines. The haemal spines of these vertebrae have been modified into hypurals by fusion with ventral radials;[5] the neural spine of the antepenultimate vertebra has been similarly modified into an epural, but the neural spine of the penultimate vertebra has been reduced to a short remnant. In addition, there are five rod-shaped radials (three dorsal, two ventral) associated with these two vertebrae: two of the dorsal radials lie above the penultimate vertebra, the other dorsal radial lies forward of the anterior epural; the ventral radials are located on either side of the anterior hypural. The terminal vertebra, or urostyle, is roughly conical in shape but bent upward. It fuses with the single, broadly triangular posterior hypural. Since the urostyle forms from a single center of ossification and fuses with a single undivided hypural, there is no indication that more than one vertebra is involved in its origin.

An examination was made of the caudal portion of a number of young hake between 150 and 200 mm. in length. The principal rays number 23 or 24 (21 or 22 branched rays, plus the adjacent unbranched ray on either side); of these, 7 or 8 are dorsal in origin, 16 are ventral in origin. The posterior 4 rays of dorsal origin are attached to the dorsal radials and the epural, one to each element. Twelve of the 16 principal rays of ventral origin are associated with hypural elements: 6 with the posterior hypural, 3 with the penultimate hypural, and 1 each with the other 3 ventral elements. Some of the more anterior caudal rays, both dorsal and ventral, appear to be articulated with unmodified neural and haemal spines; the remaining rays lie between the spines and have no basal skeletal supporting elements whatsoever.

Ventral (pelvic) fins.—At approximately 6 mm. in length, ventral buds can be discerned. Rays may be distinguished in some specimens as small as 7 mm., and the full complement has formed in all specimens 11 mm. long. Our specimens invariably had 7 ventral rays (column 11 of table 2). When the larva is 6.8 mm. in length, the ventral fin is 0.25 mm. long. At about 17.5 mm. the ventral fin is 2.5 mm. long and extends just to the anus. The posterior tip of the ventral fin reaches no farther than the anus until the larva is at least 23.8 mm. in length. A specimen 46 mm. long had ventral fins that were 5.5 mm. in length and extended 2 mm. beyond the anus. The following table shows this development:

Size of larva	Length of ventral fin
	Mm.
6.8 mm	0.3.
8.5 mm	0.5.
9.4 mm	0.8.
14.0 mm	2.1.
17.5 mm	2.5 (extends to anus).
17.6 mm	2.6 (extends to anus).
23.8 mm	3.2 (extends to anus).
46.0 mm	5.5 (extends 2 mm. beyond anus).

First dorsal fin.—The anterior rays of the first dorsal develop first; differentiation then proceeds posteriorly. About half of the specimens in the 8 to 8.5 mm. size group possess 1 or more rays in this fin, and all specimens more than 15.5 mm. have the full complement of 10 or 11 rays (column 12 of table 2). The third ray is longest; the second and fourth are nearly as long; the first ray is approximately three-fourths as long as the third. Behind the third ray the elements become progressively shorter, with the eleventh ray about one-tenth the length of the third.

Second dorsal and anal fins.—Since these fins are formed simultaneously, they will be considered together. Anal rays are found on some specimens as small as 8.5 mm., and on all specimens more than 9.2 mm. in length. The rays usually appear suddenly; the lowest number counted on larvae having differentiated anal rays is 15. The rays form from two centers, which would correspond to the divided anal fins in other gadoids. By 9.7 mm. in length, the average number of rays per specimen is 28; by 16 mm., the full complement of 41 to 43 rays is developed (column 14 of table 2).

Rays in the second dorsal are always found on specimens showing ossification of anal rays, but as few as 4 rays may be observed on some specimens. Soon, the numbers of second dorsal and anal rays correspond rather closely, although there are usually a few less second dorsal rays than anal rays. Rays in the second dorsal also

[5] We are using the same nomenclature as that given in Whitehouse (1910, p. 138) and Barrington (1937, p. 448). According to Barrington, "A hypural may be defined as a ventral element supporting one or more lepidotrichia and making contact with the notochordal axis, being subsequently attached to a vertebra; it is presumed to be composed of a haemal spine fused with a ventral radial. An epural is a dorsal element with analogous relationships, and is presumed to be composed of a neural spine fused with a dorsal radial. A radial is a dorsal or ventral element supporting one or more lepidotrichia, but not making contact with the notochordal or vertebral axis." It should be noted that this terminology differs from that used by Hollister (1936).

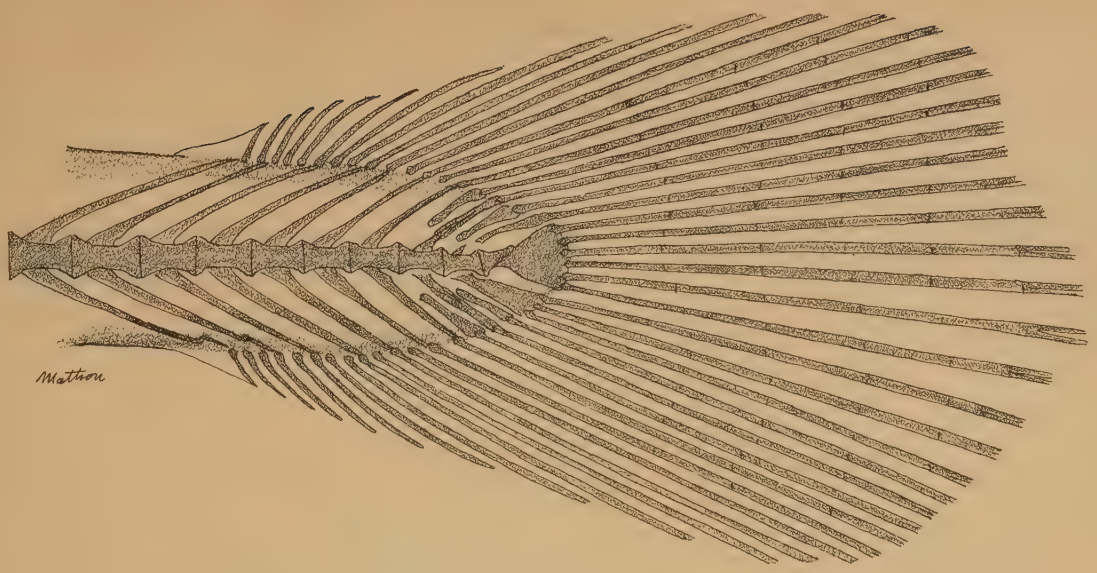

FIGURE 11.—Caudal fin and supporting skeletal structures of a 45-mm. juvenile hake.

form from two centers, which would correspond to the second and third dorsal fins in typical cods. The full complement of 40 to 42 rays in the second dorsal is found on specimens of approximately 16 mm. in length (column 13 of table 2).

The posterior rays of both the anal and the second dorsal are the last to form. The terminal ray of each is short and unbranched, differing in this respect from the majority of fishes, which have bifurcate terminal rays on dorsal and anal fins.

Pectoral fins.—The larval pectoral, which develops shortly before hatching as a fleshy-based, fan-shaped structure without rays, persists unchanged until about 17 mm. In some specimens as long as 25 mm., no rays were observed, but most specimens more than 24 mm. long have 7 or more pectoral rays. The upper rays of the pectoral form first, and differentiation then proceeds ventrally. The number of pectoral rays on 7 specimens between 23.8 and 36.5 mm. were as follows:

Size of larva	Number of pectoral rays	Size of larva	Number of pectoral rays
23.8 mm	7	29.5 mm	13
25.5 mm	7	35.5 mm	15
27.8 mm	10	36.5 mm	15
28.5 mm	12		

The full complement of 14 to 17 rays is attained between 30 and 35 mm. in length. Unfortunately, we did not have hake larvae in this size range, so that we could more exactly delimit the size at which pectoral ray formation is completed.

DISTRIBUTION AND ABUNDANCE OF LARVAE, 1951 AND 1952

The hake larvae taken in plankton collections made on survey cruises of the California Cooperative Oceanic Fisheries Investigations have been identified and enumerated routinely. The basic data on occurrence and abundance of hake larvae in 1951 and 1952 are given by Ahlstrom (1953 and 1954).

During 1951 and 1952, cruises were spaced at monthly intervals, except in December 1952. During these years the least extensive coverage was from Point Conception, Calif., to Point San Juanico, Baja California; the most extensive was from the California-Oregon border to the southern tip of Baja California; the usual coverage was from San Francisco to Point San Juanico. The coverage during 1952 was somewhat less extensive than the coverage during 1951, but was more intensive, especially within 100 to 150 miles of the coast.

Census estimates of abundance.—Estimates of abundance of hake larvae in 1951 and 1952 are given in table 5. The values represent census estimates of the number of hake larvae in different parts of the survey area at the time of each monthly cruise. Such an estimate is obtained by integrating the standard-haul totals for larvae over area, but not over time. Size of larvae is not taken into account; hence, a 3-mm. larva is given as much weight as a 30-mm. larva. Although rate of growth of hake larvae has not been determined, complete larval development must re-

TABLE 5.—*Census estimate of number of hake larvae in survey area during each cruise of 1951 and 1952*

[In billions]

	January	February	March	April	May	June	July	August	September	October	November	December	Total
1951													
Lines 60–67	84			170	6	0	0	0	0	0	0	0	260
70–77	77			501	5	9	2	0	0	0	0	0	594
80–87	1	839	4,387	4,452	94	7	0	0	0	0	1	8	9,789
90–97	5	982	1,968	1,288	34	18	0	0	0	4	0	0	4,299
100–107	1	1,422	14,888	2,384	47	3	0	0	0	0	0	0	18,745
110–117	0	197	461	338	24	34	0	1	4	1	4	12	1,076
120–127	27	318	73	169	103	25	11	0	0	0	0	0	726
130–137	36	739	612	193	37	8	1	0	0	0	0	0	1,626
Line 140 and below			120			10			0				130
Total	231	4,497	22,509	9,495	350	114	14	1	4	5	5	20	37,245
1952													
Lines 60–67				34	0	0	0	0	0	0	0		34
70–77				49	4	0	0	0	0	0	0		53
80–87	2	12	2,234	121	26	9	0	0	0	0	0		2,404
90–97	7	5,531	13,803	7,922	97	14	1	0	0	0	0		27,375
100–107	0	51	2,087	901	6	0	0	0	0	0	0		3,045
110–117	0	1,797	695	88	3	0	0	2	0	3	0		2,588
120–127	4	280	256	39	2	3	0	0	0	0	0		584
130–137	310	317	291	211	8	3	0	0	0	0	0		1,140
Line 140 and below		93											93
Total	323	8,081	19,366	9,365	146	29	1	2	0	3	0		37,316

quire more than a month; consequently we resampled some identical groups of larvae on successive cruises. With these limitations, it is obvious that a census estimate is a rather primitive measure of abundance. Nevertheless, census estimates that cover similar areas at regular intervals of time (in our case, monthly) are comparable for succeeding years, even though the estimates are relative, rather than absolute, measures of abundance.

The estimates for 1951 and for 1952 are remarkably similar—37,250 billions as compared with 37,300 billions.

Area of occurrence.—The abundance of hake larvae in different parts of the survey area may be summarized as follows:

Area	Station lines	Census estimate			
		1951		1952	
		Number	Percent	Number	Percent
		Billions		*Billions*	
North of Point Conception.	60–77	854	2.3	87	0.2
Southern California and adjacent Baja California.	80–107	32,833	88.1	32,824	88.0
Central Baja California	110–137	3,428	9.2	4,312	11.6
Southern Baja California.	140 and below	130	.4	93	.2
Total		37,245	100.0	37,316	100.0

Hake larvae were taken as far north as San Francisco, as far south as Cape San Lucas, and as far seaward as 350 miles (off southern California).

Hake larvae were taken in greatest abundance off southern California and adjacent Baja California, between Point Conception and San Quintin, station lines 80–107. Approximately 88 percent of the hake larvae collected in both 1951 and 1952 were taken in this area.

Two centers of hake abundance were encountered in 1951 (fig. 12), one just south of Point Conception (lines 80–87), the other centering off northern Baja California (lines 100–107). During 1952 (fig. 13), the center of abundance was off San Diego (lines 90–97), falling off sharply both to the north and to the south of this area.

Only a minor percentage of the hake larvae were taken to the north of Point Conception: 2.3 percent during 1951, and 0.2 percent during 1952. However, coverage of this area was inadequate, since it was not visited during February and March of either year, and coverage did not extend north of San Francisco during the hake spawning season.[6]

Season of occurrence.—The monthly abundance of hake is summarized in table 6. Hake larvae were taken in abundance only during a 3-month period, February through April. Approximately 98 percent of the hake larvae were taken during these months in both 1951 and 1952. The peak month during both seasons was March; more than

[6] The area between Point Conception and Cape Mendocino (lines 40–77) was surveyed at monthly intervals, February through September 1950, and nearly 19 percent of the hake larvae collected in 1950 were obtained in this area. However, all collections from north of Point Conception, except one occurrence off Cape Mendocino, were obtained on lines 60–77. Hence, in 1950, hake spawning north of San Francisco was negligibly small in amount.

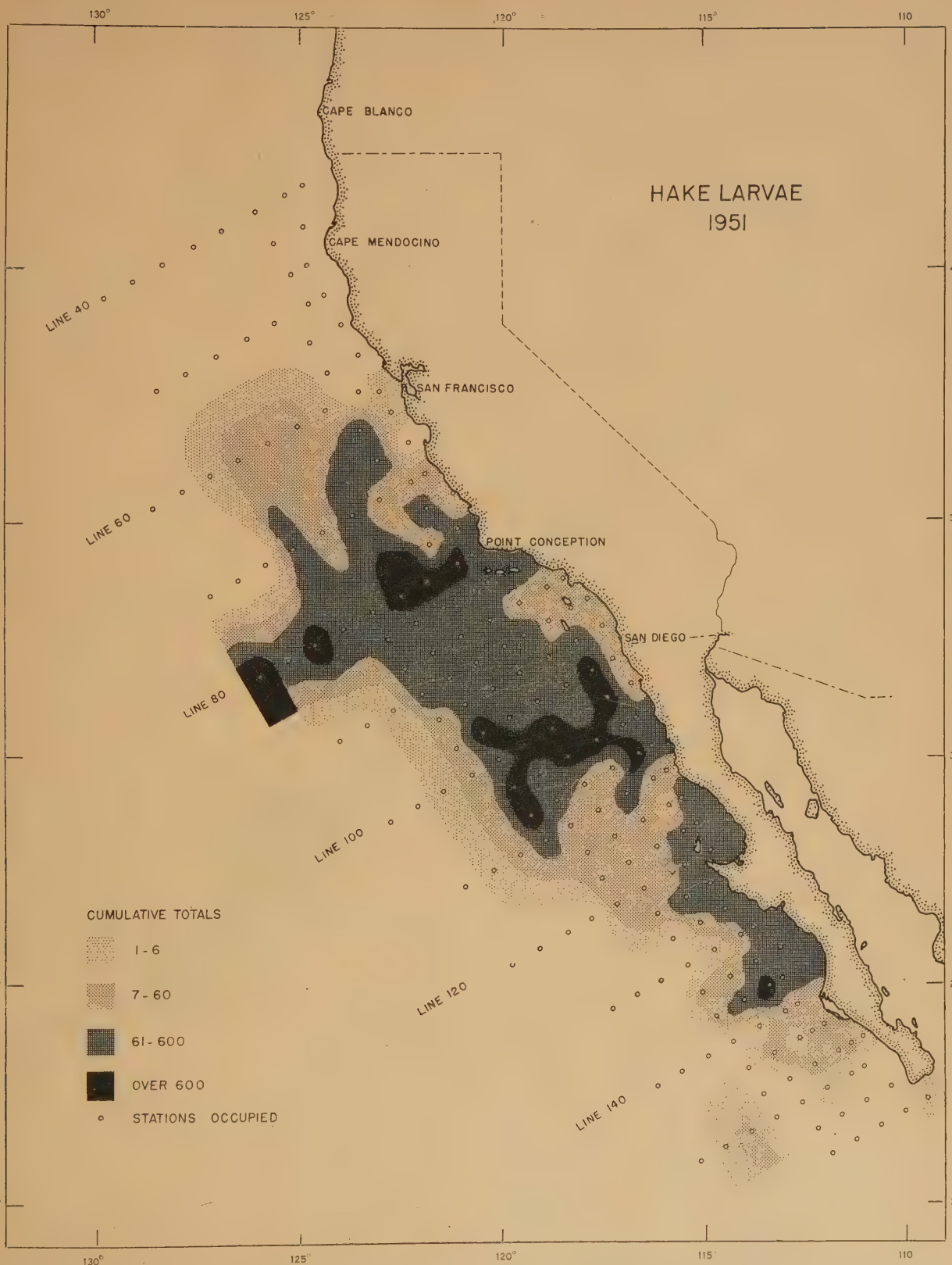

FIGURE 12.—Distribution and abundance of hake larvae in 1951. Cumulative totals represent the summation for the year of the standard-haul totals of hake larvae taken at each station on each cruise.

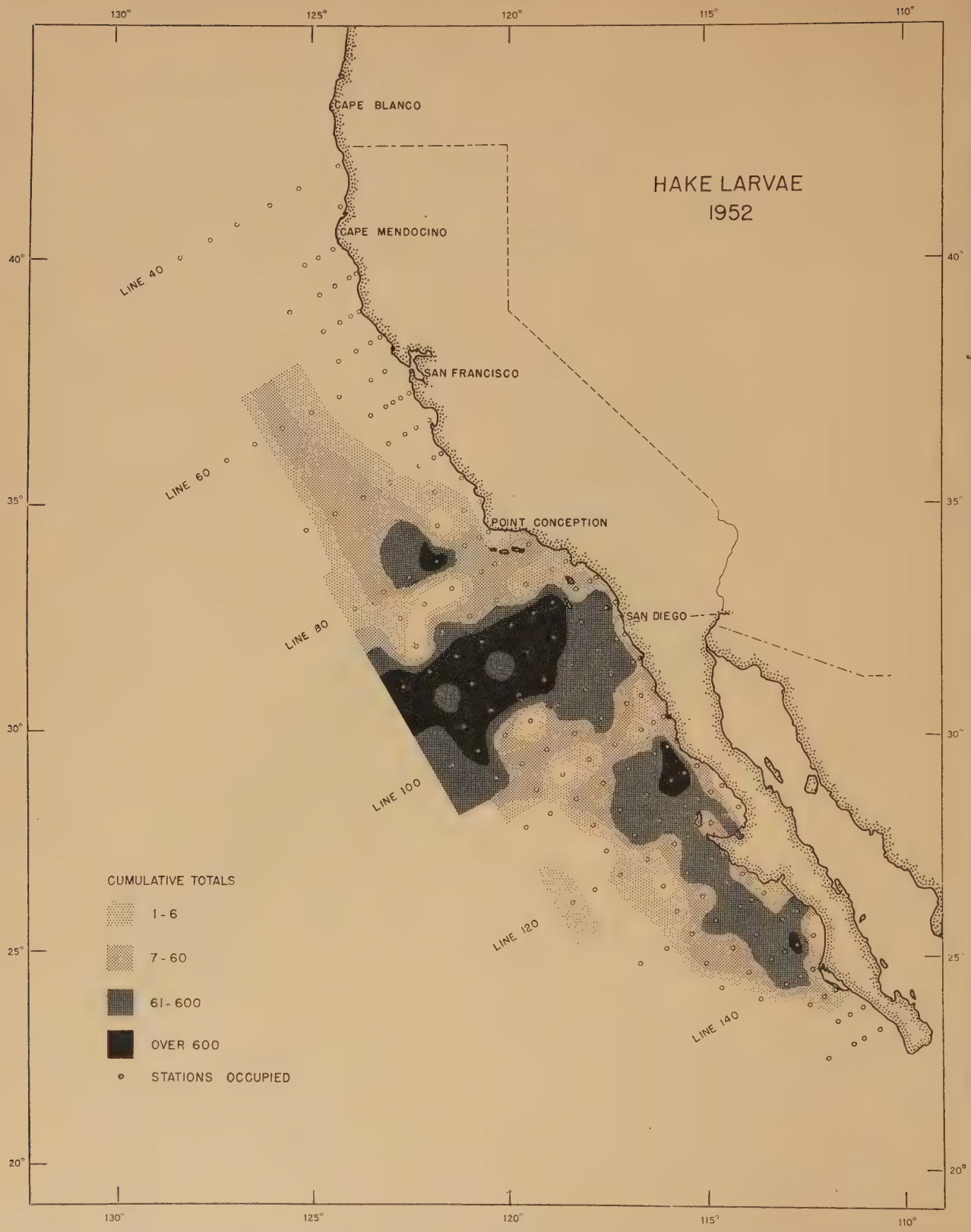

FIGURE 13.—Distribution and abundance of hake larvae in 1952. Cumulative totals represent the summation for the year of the standard-haul totals of hake larvae taken at each station on each cruise.

half of the yearly total was obtained during this month. Only negligible amounts were taken during the latter half of each year.

TABLE 6.—*Census estimates of abundance of hake larvae by months, 1951 and 1952*

Month	1951		1952	
	Number	Percent	Number	Percent
	Billions		*Billions*	
January	231	0.62	323	0.87
February	4,497	12.07	8,081	21.66
March	22,509	60.43	19,366	51.89
April	9,495	25.49	9,365	25.10
May	350	.94	146	.39
June	114	.31	29	.08
July	14	.04	1	0
August	1	0	2	.01
September	4	.01	0	0
October	5	.01	3	.01
November	5	.01	0	0
December	20	.05		
Total	37,245	99.98	37,316	100.01

The distribution and abundance of hake larvae on the monthly survey cruises made during the first 6 months of 1951 and 1952 are shown in figures 14 through 25. On most cruises, neither the north-south extent nor the offshore extent of hake larvae was delimited.

Vertical distribution.—In late March 1954, on a special cruise of the research vessel *Crest*, an area of abundant hake spawning was located about 200 miles off San Diego. To obtain information on the vertical distribution of hake eggs and larvae, two series of hauls were taken at station 94.80: one during daylight, the other during darkness. Each series consisted of 10 horizontal hauls made at successively deeper levels. The hauls were made with a net that could be opened and closed at any desired level. A comparable fishing time of 10 minutes (between opening and closing of the net) was allowed for each haul. The results are summarized in table 7.

Hake eggs were taken between 27 and 102 meters deep, hake larvae between the surface and 102 meters deep. The largest concentrations of larvae were taken between 50 and 100 meters deep. More than 98 percent of the hake larvae collected in the night series occurred at this level, with most of the larvae clustered at one depth (64 meters). The stratification was less marked in the day series: the five hauls above 50 meters averaged 46 larvae per haul, while the two hauls between 50 and 100 meters averaged 219 larvae, about 4.7 times as many. No hake larvae were taken in the two lower hauls of each series.

TABLE 7.—*Horizontal closing-net hauls made at station 94.80 on March 24–25, 1954, to study vertical distribution of hake eggs and larvae*

Midtime of haul [1]	Average depth of haul	Water temperature	Abundance of hake eggs [2]	Number of hake larvae
Day series:	*Meters*	° *C.*		
0910	0	14.1	0	65
0940	7	14.1	0	85
1005	18	14.1	0	24
1025	28	14.0	0	13
1105	41	14.0	C	45
1140	53	13.8	A	156
1230	68	13.2	A	282
1305	102	11.1	R	22
1350	135	9.7	0	0
1425	201	8.6	0	0
Night series:				
2030	0	14.3	0	15
2100	7	14.3	0	6
2125	17	14.3	0	4
2145	27	14.3	R	1
2310	42	14.3	A	2
2330	52	14.3	A	92
0000	64	14.1	A	1,619
0025	101	10.8	R	8
0135	127	9.9	0	0
0215	200	8.7	0	0

[1] Pacific standard time.

[2] Hake eggs were not counted. Symbols used to indicate abundance: R=few; C=common; A=abundant.

In addition to the above series, some hake larvae have been collected incidentally in hauls made for studying the vertical distribution of sardine eggs and larvae. These were taken off southern California, in 1941 and subsequently, all within a radius of 120 miles of San Diego. The hake larvae taken in these collections are listed in table 8.

TABLE 8.—*Occurrence of hake larvae in closing-net hauls made to investigate the vertical distribution of fish eggs and larvae*

[All hauls made off southern California]

Middepth of haul	Number of larvae									
	Series 1832 Apr. 10, 1941 1100–1530	Series 2032 May 2, 1941 0800–1400	Series 2043 May 2, 1941 2000–2400	Series 2046 Apr. 30, 1941 1700–2100	Series 2452N [1] June 17, 1941 2200–0330	Series 2452D [1] June 18, 1941 0900–1400	Series 2463D June 20, 1941 0800–1430	Series 9138N [1] June 12, 1952 2130–0430	Series 9138D [1] June 13, 1952 0900–1500	Total
3 meters	0	0	0	0	0	0	0	0	0	
10 meters	------	0	0	0	0	0	0	0	0	
20 meters	0	0	0	0	0	0	0	0	0	0
27 meters	0	0	3	0	0	1	0	0	0	4
40 meters	3	0	5	2	2	3	0	0	3	18
57 meters	10	14	9	20	0	4	0	2	2	61
75 meters	9	7	4	13	1	0	0	12	0	46
100 meters	------	------	1	------	0	0	0	0	0	1
140 meters	------	------	------	------	------	0	1	------	0	1
Total	22	21	22	35	3	8	1	14	5	131

[1] Series repeated in same locality, N=at night, D=during daylight.

Hake were obtained in seven series in small numbers (1 to 35 larvae per series). The depth distribution of these samples is similar to that obtained at station 94.80: most larvae were obtained between 50 and 100 meters; however, no larvae were taken above 27 meters deep.

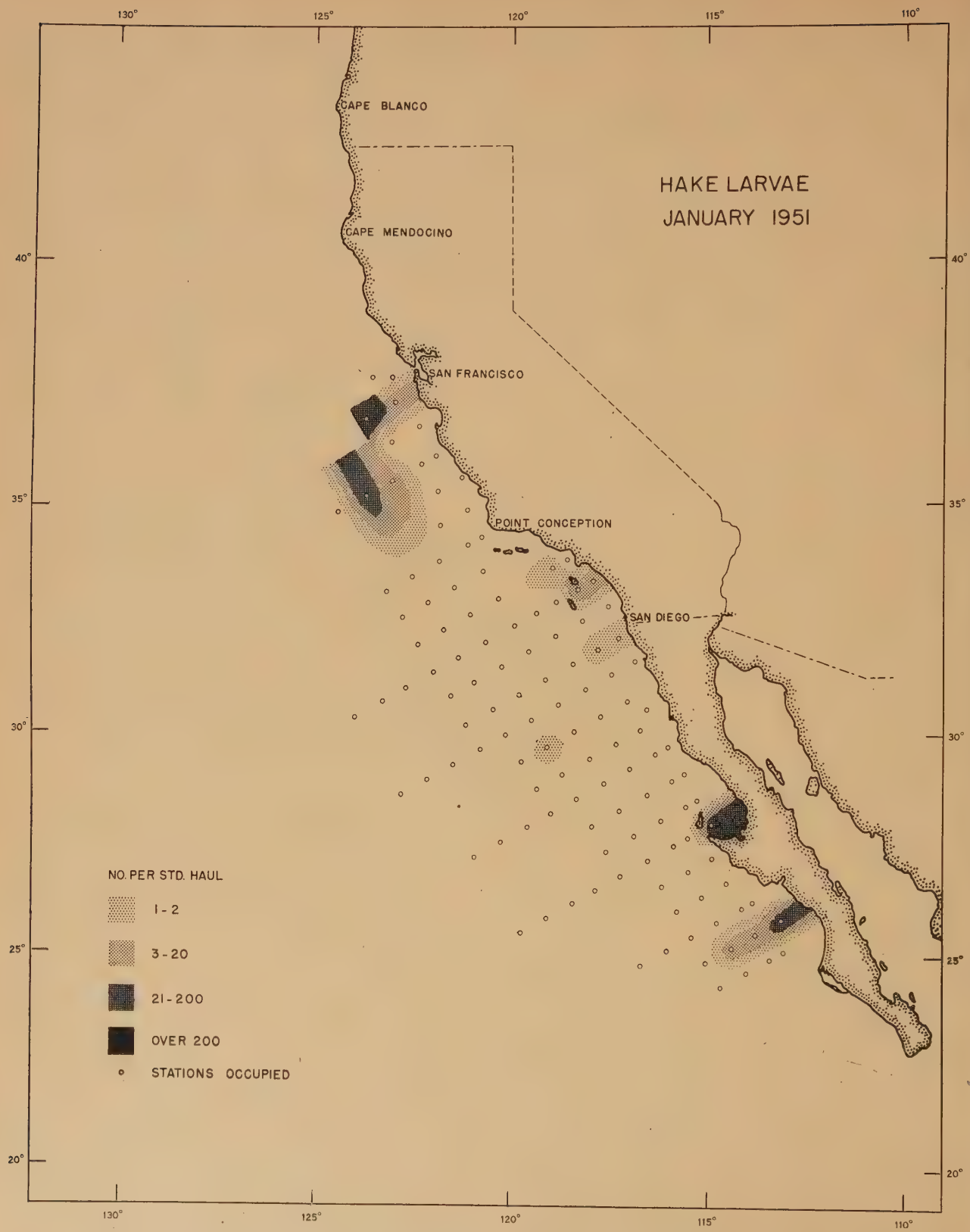

FIGURE 14.—Distribution and abundance of hake larvae during January 1951.

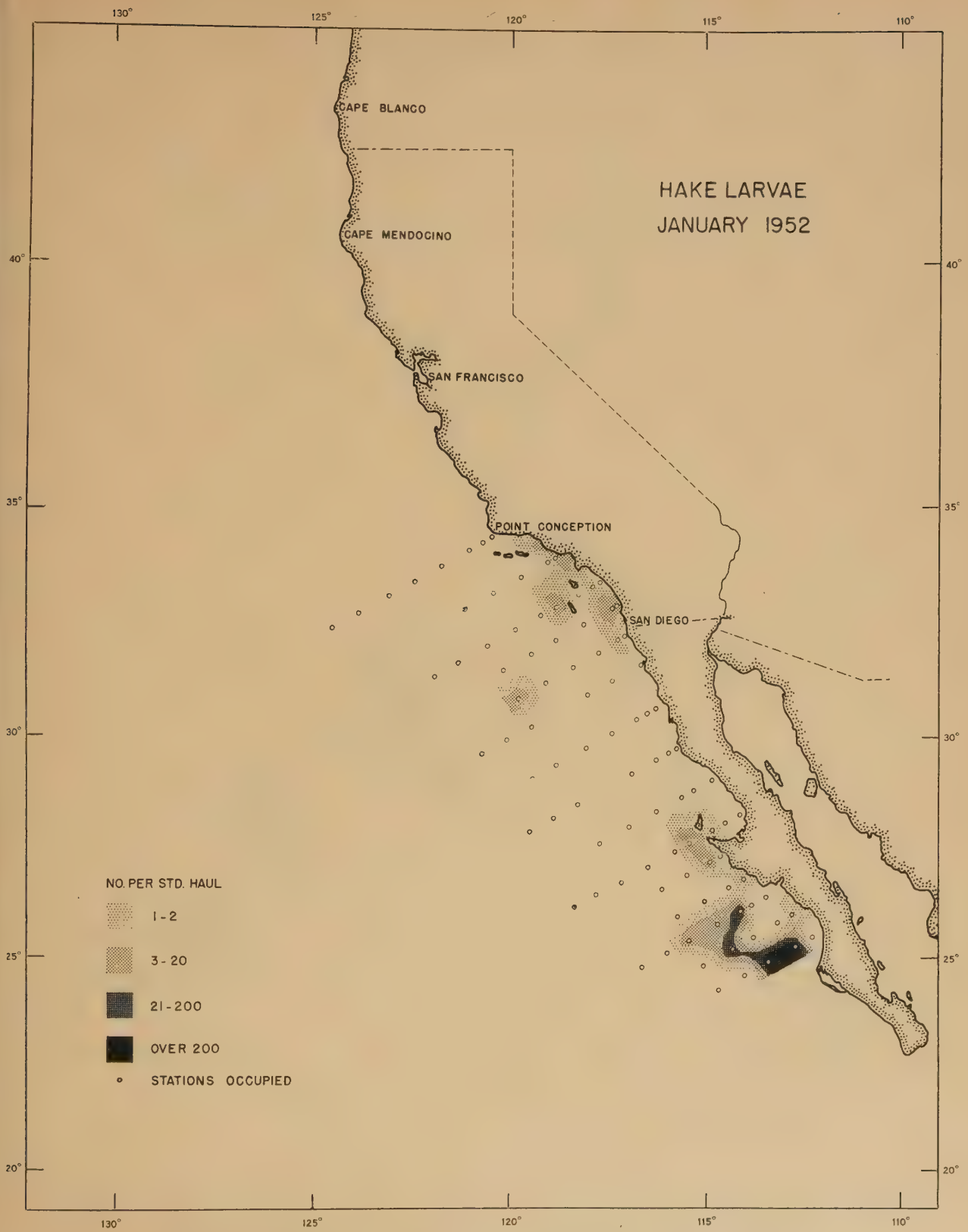

FIGURE 15.—Distribution and abundance of hake larvae during January 1952.

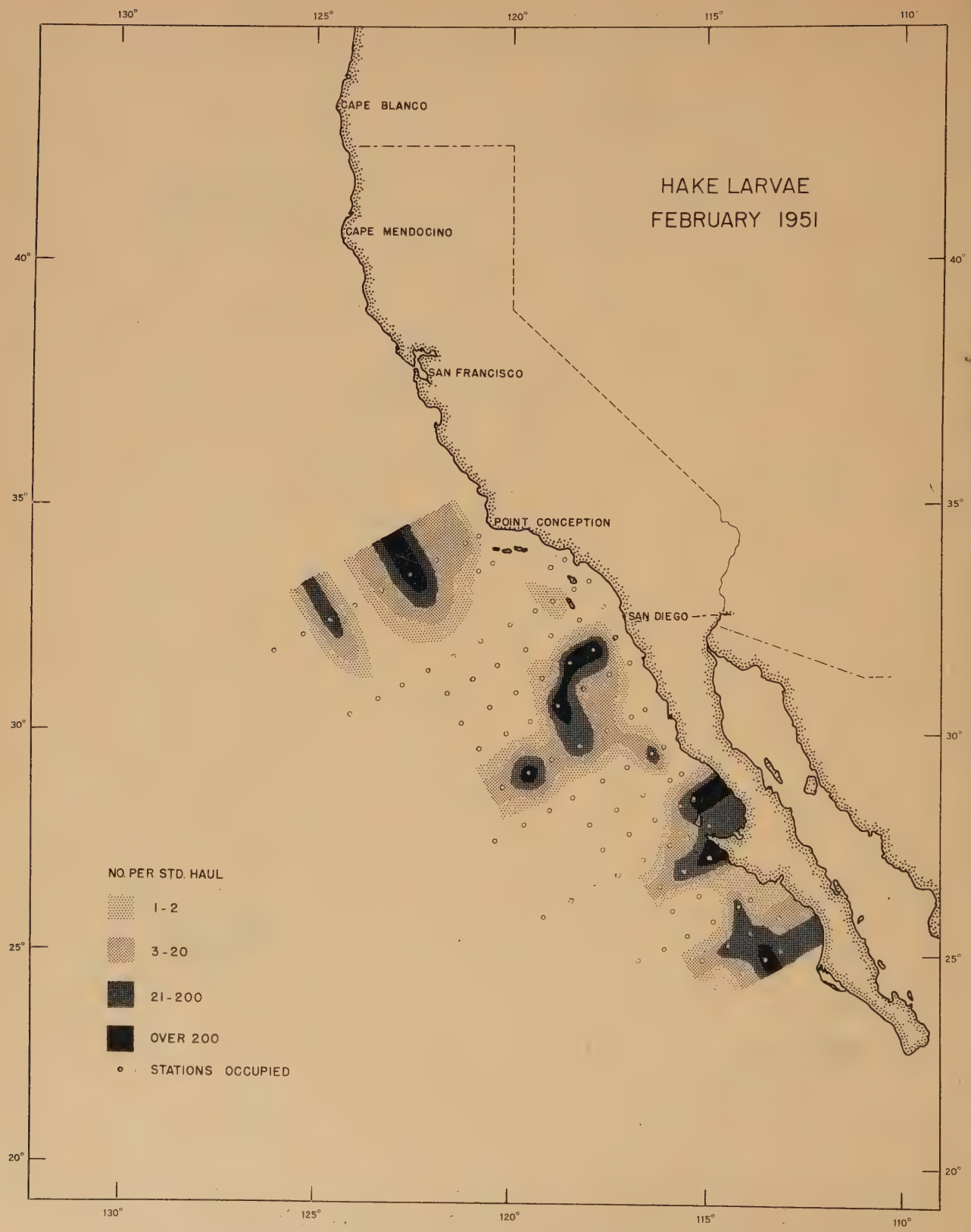

FIGURE 16.—Distribution and abundance of hake larvae during February 1951.

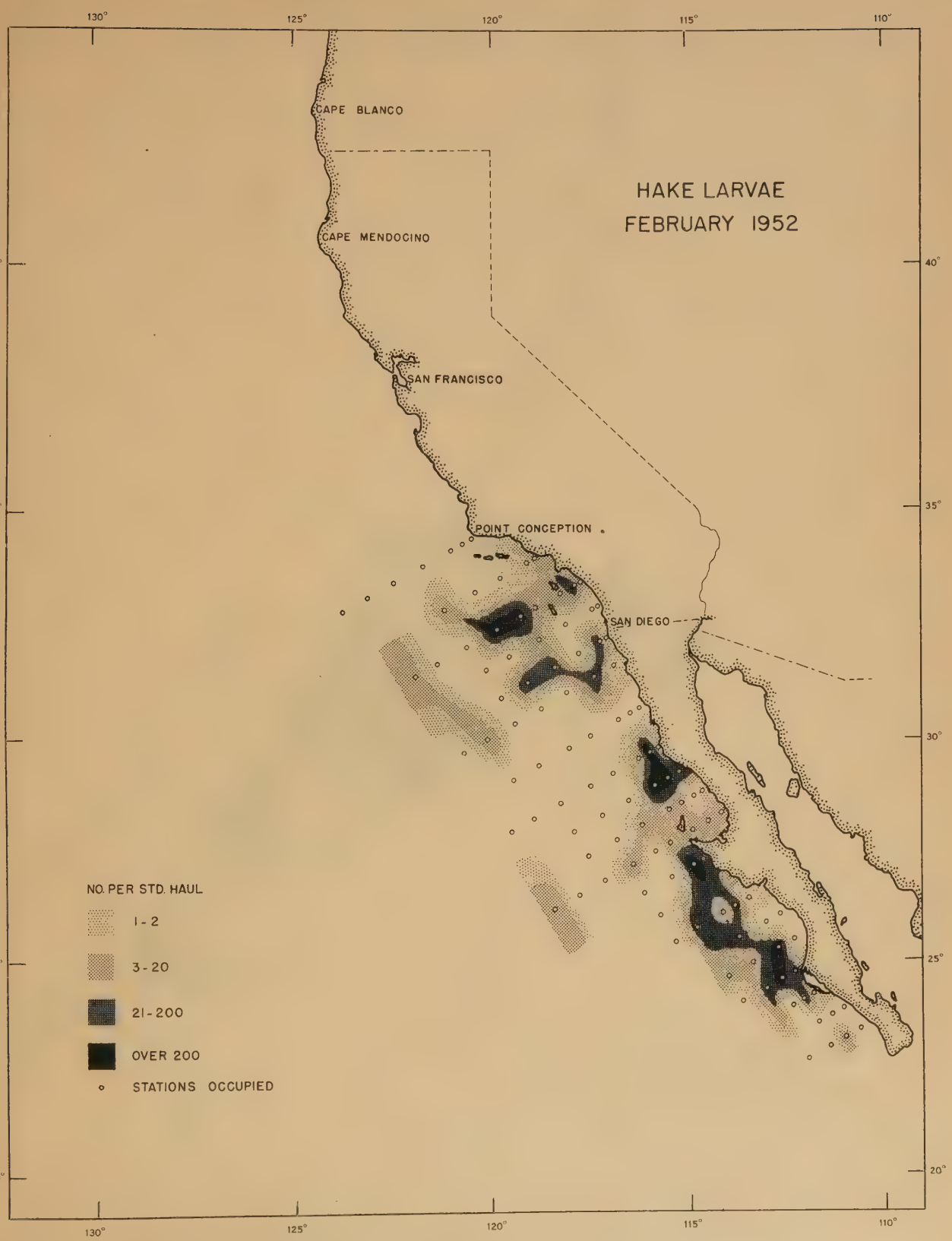

FIGURE 17.—Distribution and abundance of hake larvae during February 1952.

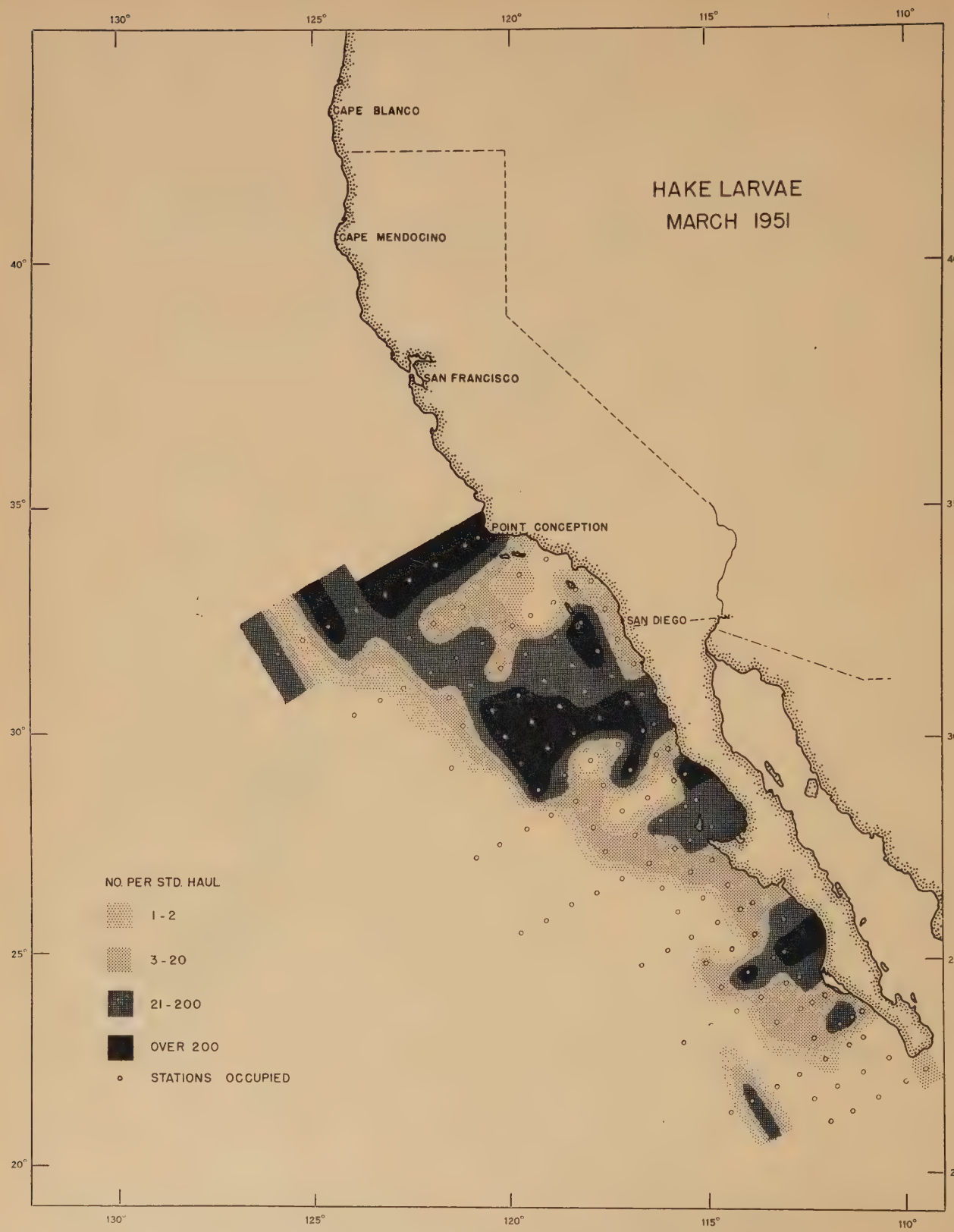

FIGURE 18.—Distribution and abundance of hake larvae during March 1951.

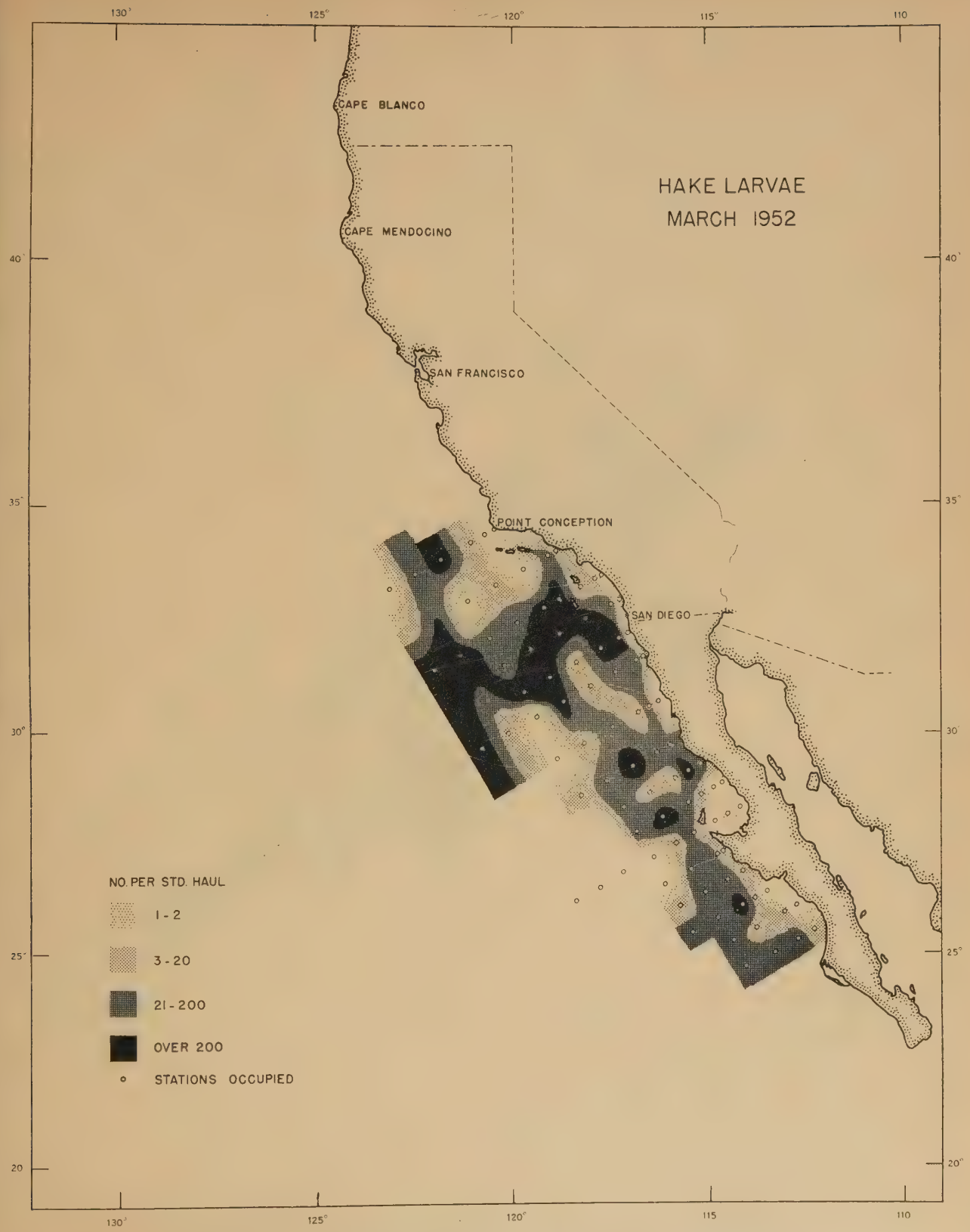

FIGURE 19.—Distribution and abundance of hake larvae during March 1952.

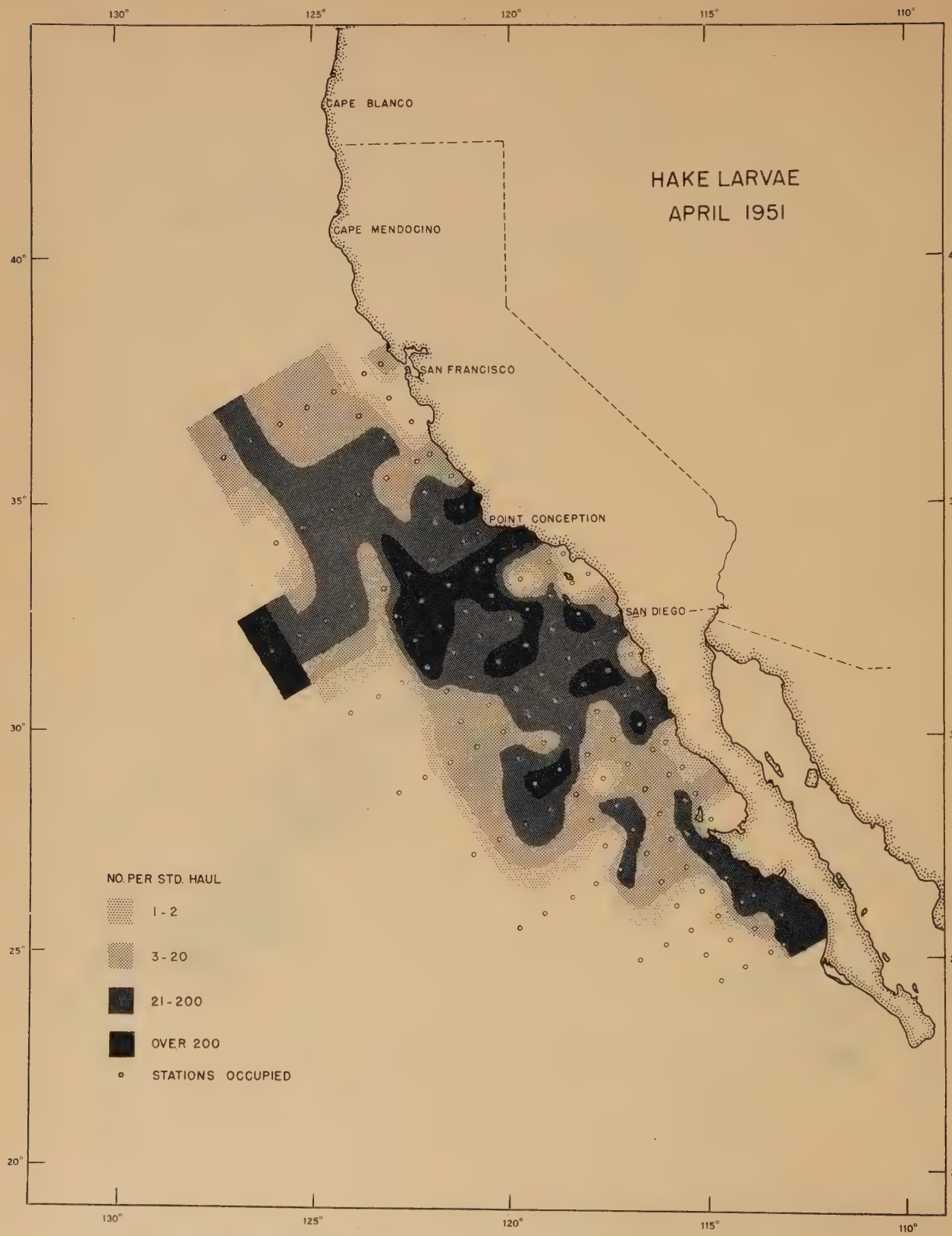

FIGURE 20.—Distribution and abundance of hake larvae during April 1951.

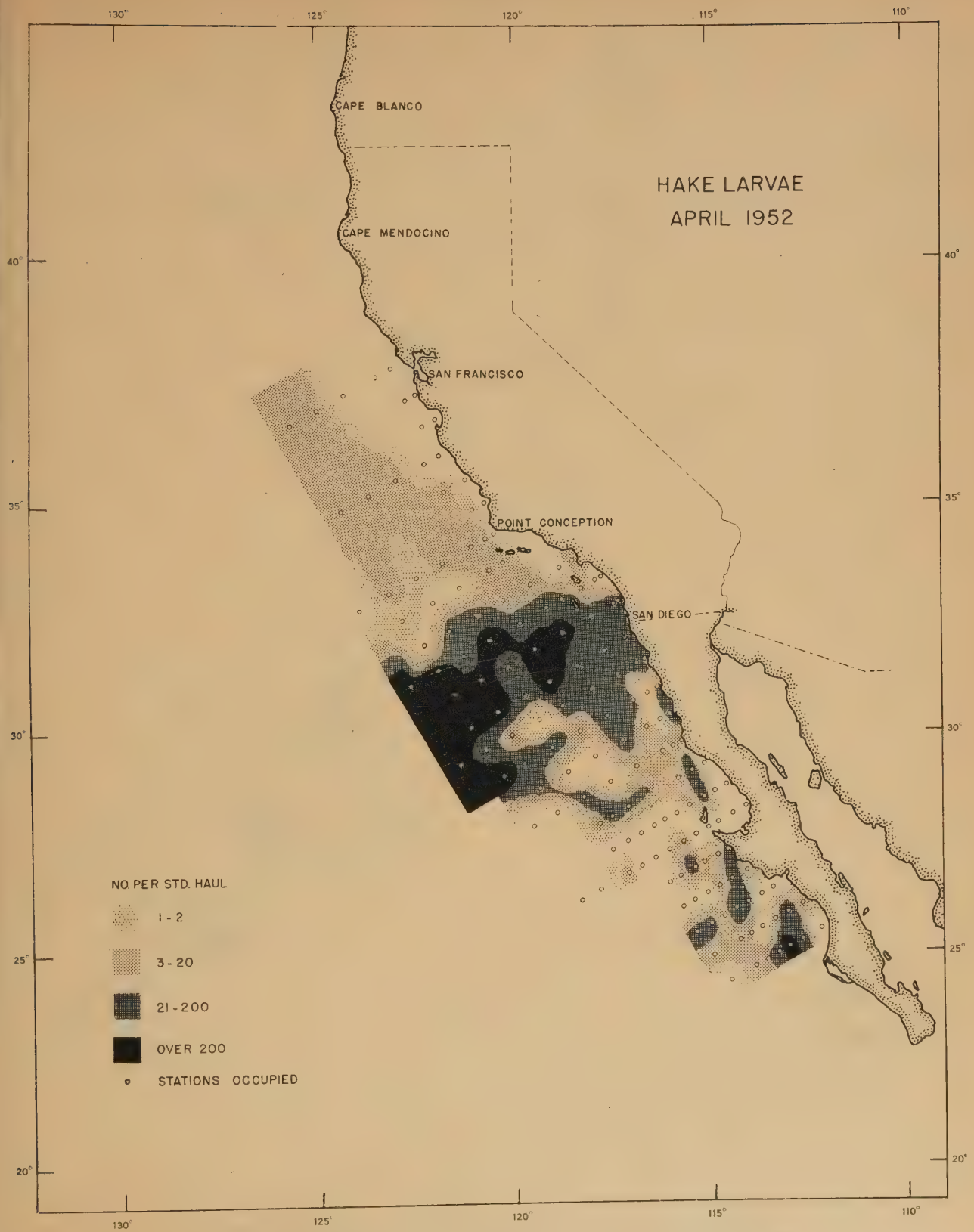

FIGURE 21.—Distribution and abundance of hake larvae during April 1952.

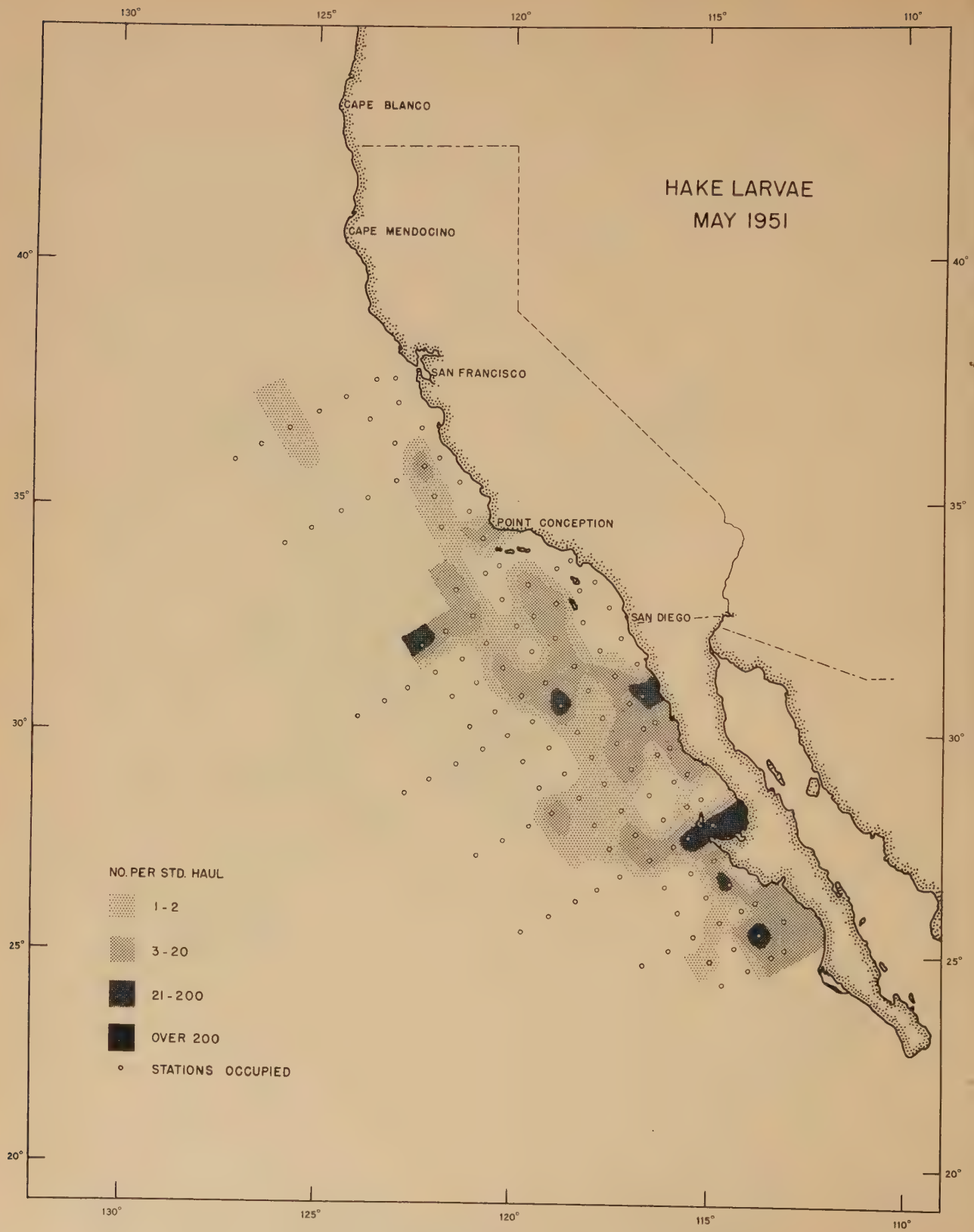

FIGURE 22.—Distribution and abundance of hake larvae during May 1951.

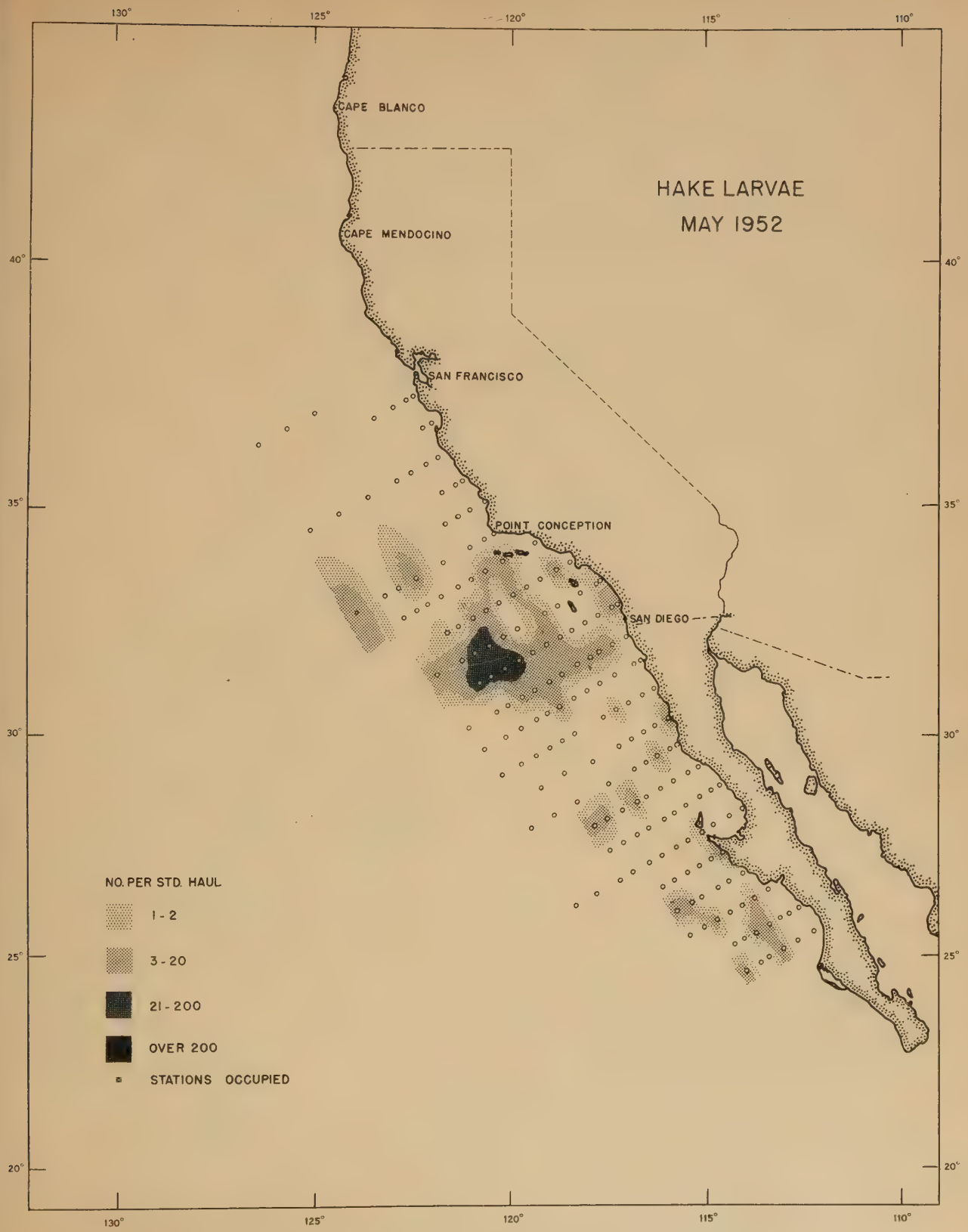

FIGURE 23.—Distribution and abundance of hake larvae during May 1952.

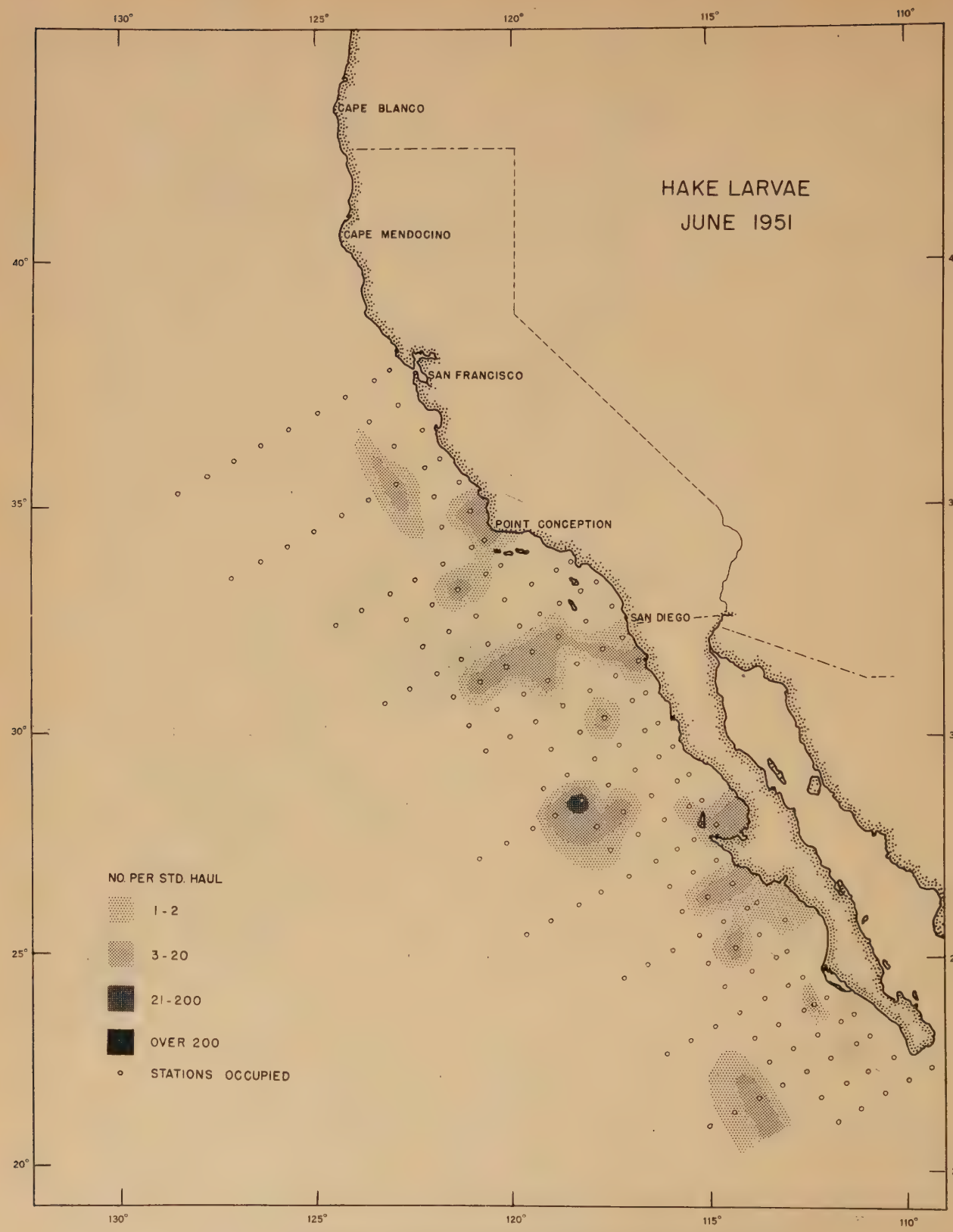

FIGURE 24.—Distribution and abundance of hake larvae during June 1951.

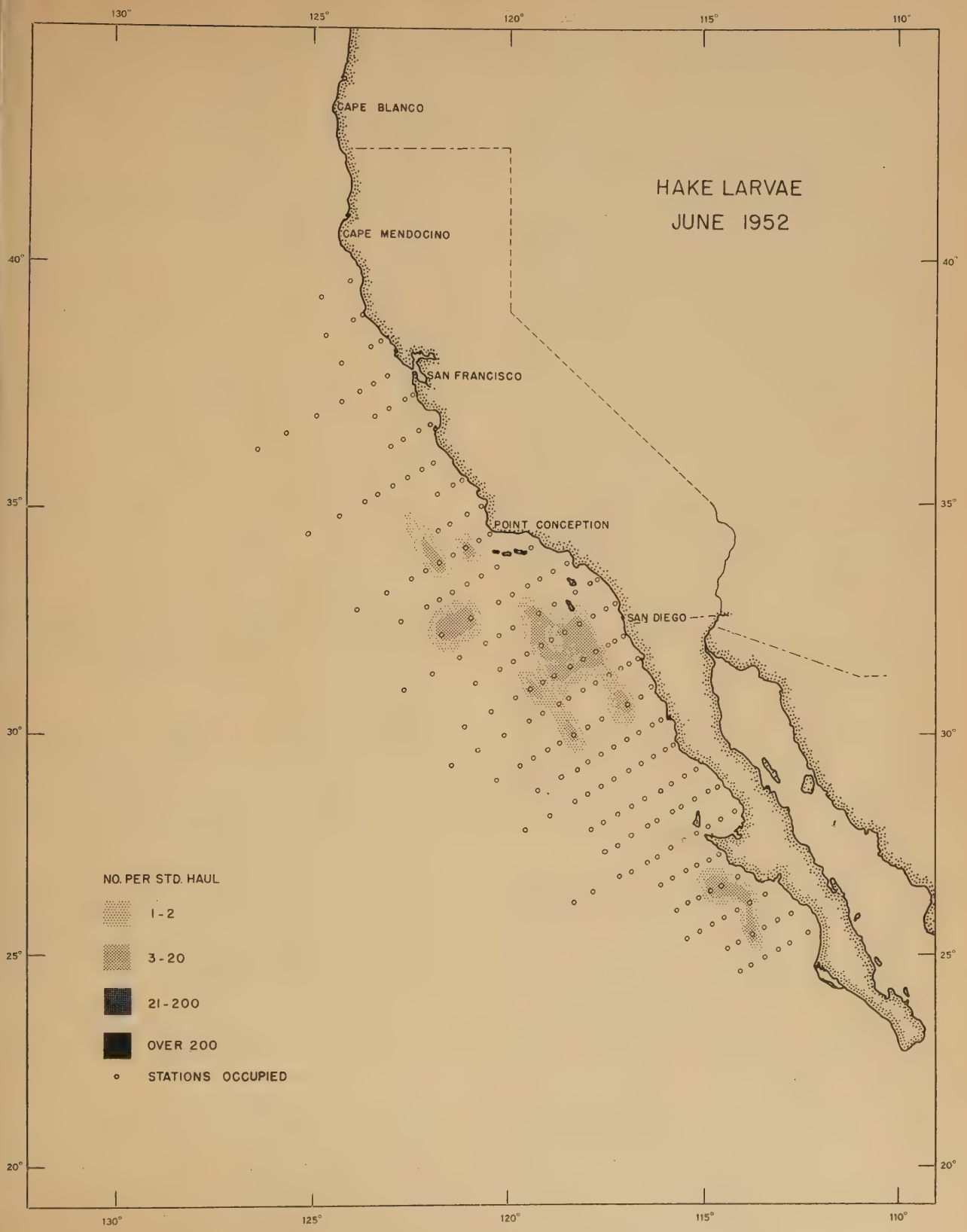

FIGURE 25.—Distribution and abundance of hake larvae during June 1952.

Relation to temperature.—The temperature range over which hake larvae were taken at station 94.80 was between 10.8° and 14.3° C., and in the other depth-distribution series it was between 11.0° and 15.4° C., with most larvae occurring at temperatures between 11.5° and 14.3°. The largest concentrations of hake larvae occurred near to or within the thermocline.

With the limited information on hand about the depth distribution of hake larvae, it is difficult to relate the distribution of hake larvae taken on survey cruises to temperature. In making such a comparison, it is desirable that the temperature at each station be expressed as a single value. This value can be either the average of a depth zone (the stratum within which most larvae occur), or the temperature at a selected depth (preferably the depth at which the largest concentrations of larvae occur). A problem arises in selecting either a depth zone or a particular depth, for there is some evidence that the depth distribution as determined from special studies (tables 7 and 8) may not be typical of the general distribution of hake larvae. The yearly catch of hake larvae was increased several fold when the average depth of hauls was increased from approximately 68 to 135 meters, indicating that a larger proportion of hake larvae occur between 68 and 135 meters deep than in the stratum above. Obviously, more work is needed to determine the usual depth zone within which hake occur, and the relation of the depth distribution to such features as thermocline depth and latitude. Consequently, we have not tried to obtain the average temperature of a depth zone.

In making temperature observations at a hydrographic station, thermometers are usually spaced at only four depths in the stratum between 50 and 150 meters, these depths being 50, 75, 100, and 150 meters. In selecting a level that will represent the usual concentration of hake larvae, and yet have a directly determined, rather than an interpolated, temperature value, one of these four depths should be used. We have selected the 75-meter level. The abundance of larvae in relation to the temperature at this depth is summarized in table 9. The large concentrations of hake larvae (1,001 or more per standard haul) were taken over a 4.5-degree temperature range, 10.6° to 15.0° C. This temperature range is very similar to that found at the depths where hake larvae were obtained during vertical distribution studies. The overall temperature range at all stations at which hake larvae were obtained was greater, being from 8.6° to 18.5° C. Only about 4 percent of the occurrences were at temperatures greater than 16° C., however.

TABLE 9.—*Relation between water temperature at 75-meter depth and abundance of hake larvae, 1951 and 1952*

Temperature at 75-meter level	Number of standard hauls that collected—				Total number of hauls
	1 to 10 larvae	11 to 100 larvae	101 to 1,000 larvae	1,001 or more larvae	
Centigrade					
8.6°–9.0°	4	0	0	0	4
9.1°–10.0°	37	29	4	0	70
10.1°–11.0°	56	30	16	1	103
11.1°–12.0°	41	42	24	6	113
12.1°–13.0°	38	18	17	9	82
13.1°–14.0°	28	20	19	4	71
14.1°–15.0°	27	27	23	7	84
15.1°–16.0°	13	16	5	0	34
16.1°–17.0°	9	5	1	0	15
17.1°–18.0°	5	2	0	0	7
18.1°–18.5°	2	0	0	0	2
Total	260	189	109	27	585

LITERATURE CITED

AHLSTROM, ELBERT H.

1943. Studies on the Pacific pilchard or sardine (*Sardinops caerulea*); 4. Influence of temperature on the rate of development of pilchard eggs in nature. U. S. Dept. Interior, Fish and Wildlife Service, Spec. Sci. Rept. No. 23. 26 pp.

1953. Pilchard eggs and larvae and other fish larvae, Pacific coast—1951. U. S. Dept. Interior, Fish and Wildlife Service, Spec. Sci. Rept.—Fisheries No. 102 55 pp.

1954. Pacific sardine (pilchard) eggs and larvae and other fish larvae, Pacific coast—1952. Spec. Sci. Rept.—Fisheries No. 123. 76 pp.

AHLSTROM, ELBERT H., and ORVILLE P. BALL.

1954. Description of eggs and larvae of jack mackerel (*Trachurus symmetricus*) and distribution and abundance of larvae in 1950 and 1951. U. S. Dept. Interior, Fish and Wildlife Service, Fishery Bull., No. 97, vol. 56, pp. 209–245.

BARRINGTON, E. J. W.

1937. The structure and development of the tail in plaice (*Pleuronectes platessa*) and the cod (*Gadus morrhus*). Quart. Jour. Micr. Sci., vol. 79, pp. 447–469.

BIGELOW, HENRY B., and WILLIAM W. WELSH.

1925. Fishes of the Gulf of Maine. U. S. Bureau of Fisheries, Bull., vol. 40 (1924), part I. 567 pp.

BIGELOW, HENRY B., and WILLIAM C. SCHROEDER.

1953. Fishes of the Gulf of Maine. U. S. Dept. Interior, Fish and Wildlife Service, Fishery Bull., No 74, vol. 53. 577 pp.

CLOTHIER, CHARLES R.
1950. A key to some southern California fishes based on vertebral characters. California Dept. Fish and Game, Fish Bull. No. 79. 83 pp.

D'ANCONA, UMBERTO.
1933. Gadidae in uova, larve e stadi giovanili di Teleostei. Fauna e Flora del Golfo di Napoli, Monogr. 38, pp. 178–255.

EHRENBAUM, E.
1905–1909. Eier und Larven von Fischen. Nordisches Plankton, vol. 1. 414 pp.

EVANS, H. E.
1948. Clearing and staining small vertebrates in toto for demonstrating ossification. Turtox News, vol. 26, No. 2, pp. 42–47.

FRY, DONALD H., JR.
1936. A description of the eggs and larvae of the Pacific mackerel. California Fish and Game, vol, 22, No. 1, pp. 27–29.

HART, T. J., and N. B. MARSHALL.
1951. Breeding ground of pilchards off the coast of south–west Africa. Nature, vol. 168, p. 272.

HOLLISTER, GLORIA.
1934. Clearing and dyeing fish for bone study. Zoologica, vol. 12, pp. 89–101.
1936. Caudal skelton of Bermuda shallow water fishes. I. Order Isospondyli: Elopidae, Megalopidae, Albulidae, Clupeidae, Dussumieriidae, Engraulidae. Zoologica, vol. 21, pp. 257–290.

KUNTZ, ALBERT, and LEWIS RADCLIFFE.
1917. Notes on the embryology and larval development of twelve teleostean fishes. U. S. Bureau of Fisheries, Bull., vol. 35, pp. 87–134.

MATTHEWS, J. P., and B. V. D. DE JAGER.
1951. The development of the Cape stockfish (*Merluccius capensis*). Union of South Africa, Dept. of Commerce and Industry, Fish. and Mar. Biol. Survey Div., Investigational Rept. No. 13. 10 pp.

NORMAN, J. R.
1937. Coast fishes. Part II. The Patagonian Region. Discovery Repts., vol. 16, pp. 1–150.

PEARSON, JOHN C.
1941. The young of some marine fishes taken in Lower Chesapeake Bay, Virginia, with special reference to the Gray Sea Trout (*Cynoscion regalis* (Bloch)). U. S. Dept. Interior, Fish and Wildlife Service, Fishery Bull., No. 36, vol. 50, pp. 79–102.

RAFFAELE, F.
1888. Le uova galleggianti e le larve dei Teleostei nel Golfo di Napoli. Mitt. Zool. Station Neapel, vol. 8, pp. 1–84.

SCHMIDT, JOHS.
1907. On the post-larval development of the hake (*Merluccius vulgaris* Flem.). Meddel. fra. Kom. f. Havunders., Serie: (Fiskeri) vol. 2, No. 7. 9 pp.

WHITEHOUSE, R. H.
1910. The caudal fin of fishes (preliminary paper). Proc. Royal Soc. London, vol. 82B, pp. 134–143.

ADDENDUM

The interesting paper on American hakes by Ginsburg (Whitings on the coasts of the American continents, U. S. Dept. Interior, Fish and Wildlife Service, Fish. Bull. 96, vol. 56, pp. 187–208) was not seen by the authors until the present paper was in page proof. Ginsburg reports two species of hake from off western North America, *Merluccius productus* and *M. angustimanus* Garman. Eight specimens of the latter species, collected between Del Mar, Calif., and Panama were examined by Ginsburg.

The meristic characters of the two species, as given by Ginsburg, are as follows:

	M. productus	*M. angustimanus*
First dorsal	10–12	11 or 12
Second dorsal	39–44	36–39
Anal	41–44	37–40
Pectoral	14–16	15–17
Gill rakers	4–5+13–18	3–5+12–14
Scales (lateral line)	147–166	130–149

Although not mentioned in the body of the paper, a careful examination was made of our collections of hake eggs and larvae to determine whether one or two species were represented. We could not find evidence of more than one species. All specimens on which the dorsal and anal fins were fully developed had 40 to 42 rays in the second dorsal and 40 to 43 rays in the anal. Thus, our specimens were outside the range given by Ginsburg for *M. angustimanus*, but within the range associated with *M. productus*. Apparently, *M. angustimanus* either does not spawn within the area routinely surveyed on cruises of the California Cooperative Oceanic Fisheries Investigations, or the spawning takes place at a deeper level than that sampled by the hauls.